THE PHYLOGENY OF THE OREODONTS

PARTS 1 AND 2

C. BERTRAND SCHULTZ AND
CHARLES H FALKENBACH

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PART 1: MERYCOIDODONTINAE, EPOREODONTINAE, AND LEPTAUCHENIINAE, THREE SUBFAMILIES OF OREODONTS, WITH AN APPENDIX TO THE REVISION OF THE MERYCOIDODONTIDAE

PART 2: SUMMARY AND CONCLUSIONS CONCERNING THE MERYCOIDODONTIDAE

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EIGHTH CONTRIBUTION TO THE REVISION OF THE OREODONTS
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[1] Chadron faunal zones after Osborn, 1929, p. 57; see chart 1 of present paper.
[2] Brule faunal zones are divisions by the present writers; see chart 1.

[1] See discussion of the correlation of the John Day deposits with those of the Harrison (p. 199).

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INTRODUCTION TO PART 1

REPORT NUMBER EIGHT (Part 1) in the revision of the oreodonts (Merycoidodontidae) by the present writers deals with the last three of the 11 subfamilies (9, Merycoidodontinae; 10, Eporeodontinae; and 11, Leptaucheniinae) and with supplementary evidence concerning six previously revised subfamilies (Merycochoerinae, Ticholeptinae, Merychyinae, Desmatochoerinae, Miniochoerinae, and Oreonetinae).[1]

The subfamily Merycoidodontinae embraces six genera (including five new) and six new subgenera, all closely related: *Merycoidodon, M. (Anomerycoidodon), M. (Blickohyus), Paramerycoidodon, P. (Barbourochoerus), P. (Gregoryochoerus), Otionohyus, O. (Otarohyus), Genetochoerus, G. (Osbornohyus), Pseudogenetochoerus,* and *Epigenetochoerus.* The size ranges from the smallest of the subfamily, *Genetochoerus periculorum* (from the lower part of the Brule), with a skull length approximately equal to that of examples of *Miniochoerus cheyennensis* (from the upper part of the Brule), to the largest, *Paramerycoidodon (Barbourochoerus) major* (from the upper Brule), with a skull comparable in length to that of *Desmatochoerus (Paradesmatochoerus) monroecreekensis* (from the Monroe Creek). The subfamily is represented by 1015 skulls, mandibular rami, and skeletal elements (690 F:A.M. specimens, 100 U.N.S.M., and 225 in various other institutions), which are described or listed in this report. Sixty-four of these specimens are illustrated in 23 text figures (including seven refigured types), representing 26 species (16 new) and four subspecies (three new). The drawings of the skulls, jaws, and skeletal elements are reproduced at one-half natural size, but the lateral and occlusal views of the third upper molars in figures 48-53 are illustrated at natural size.

The figures of the Merycoidodontinae illustrate the range in size, shape, and proportions of the skulls, mandibular rami, and limb elements. The outstanding difference between the genera (from the Chadron and "Zone A" of the Brule) and the subgenera (from "Zone B" of the Brule and higher horizons) is that the former possess small (minute) bullae, whereas the latter have large, inflated ones. It is also noted that the skulls representing genera from "Zone A" and those of the subgenera from "Zone B" are similar in size, but skulls from zones "C" and "D" are noticeably larger. There is a gradual increase in size of the skulls from the latter zones.

The subfamily Eporeodontinae embraces two related genera (one is new) and a new subgenus, *Eporeodon, E. (Paraeporeodon)* and *Dayohyus,* all confined to the John Day deposits of Oregon. The size range of the subfamily is limited, and the smallest, *Dayohyus trigonocephalus,* has a skull length approximately equal to that of examples of *Promesoreodon scanloni* from "Zone D" of the Brule. The subfamily is represented by 208 skulls, mandibular rami, and skeletal elements, which are described or listed in this report. Fourteen of these specimens are illustrated in seven text figures (including four refigured types), representing seven species (two of which are new) and a subspecies. The drawings are reproduced at one-half natural size.

The illustrations of the Eporeodontinae show the size, shape, and proportions of the skulls, mandibular rami, and limb elements. The geologic occurrences of the John Day oreodonts in most cases are questionable. A suggested relationship between the forms is shown in chart 1 (p. 22).

The subfamily Leptaucheniinae embraces seven related genera (three of which are new): *Sespia, Megasespia, Pithecistes, Leptauchenia, Cyclopidius, Hadroleptauchenia,* and *Pseudocyclopidius.* The size ranges from the smallest of the subfamily, *Sespia marianae* (from the Gering), with a skull length approximating that of *Bathygenys alpha* (from "Zone B" of the Chadron), to the largest, *Pseudocyclopidius lullianus expiratus* (from the Monroe Creek), with a skull comparable in length with that of

[1] Those subfamilies already described by the present writers are: subfamily 1, Merycochoerinae (1940, p. 213); subfamily 2, Ticholeptinae (1941, p. 1); subfamily 3, Merychyinae (1947, p. 161); subfamily 4, Promerycochoerinae (1949, p. 73); subfamily 5, Phenacocoelinae (1950, p. 91); subfamily 6, Desmatochoerinae (1954, p. 143); subfamily 7, Miniochoerinae (1956, p. 391); and subfamily 8, Oreonetinae (1956, p. 453).

Merychyus arenarum (from the lower Marsland). The subfamily is represented by 1028 skulls, mandibular rami, and skeletal elements (559 F:A.M. specimens, 259 U.N.S.M., and 170 in other institutions), which are described or listed in this report. Fifty of these listed specimens are illustrated in 13 text figures (including nine refigured types), representing 28 species (17 of which are new). The drawings are reproduced at one-half natural size.

The illustrations of the Leptaucheniinae show the size, shape, and proportions of the skulls, mandibular rami, and limb elements. In contrast to other subfamilies of the oreodonts, the leptauchenins possess large, well-inflated bullae throughout the geologic history of the subfamily (from "Zone A" of Brule through the Monroe Creek), whereas in other subfamilies the bullae of forms from "Zone A" are small (minute). Also noteworthy is the large nasal-facial vacuity which extends posteriorly through the anterior wall of the orbit (see fig. 54). This character is not present in other oreodonts, nor in mammals in general. The dentition is outstanding, as it includes the most hypsodont molars (in *Sespia*) of all artiodactyls. In fact, the last molars are proportionally more hypsodont than even in the Pleistocene and Recent horses (fig. 42).

Acknowledgments

The drawings for Parts 1 and 2 of the present report were executed by Miss Hazel de Berard, Miss Ellen Forsythe, Mr. Raymond J. Gooris, Mrs. Elizabeth Bell, and Mr. Evan Palmer, all of the Frick Laboratory. Mr. Gooris also prepared the graphic charts and aided in other ways in the preparation of the final manuscript.

The writers are grateful to all who have helped to make these studies possible, particularly those whose aid and encouragement have been acknowledged in the previously published revisions[1] of the subfamilies of the Merycoidodontinae.

Mr. Childs Frick and his associate Dr. Harold E. Anthony from the Frick Laboratory were most helpful with their counsel and support. Additional appreciation is due to staff members at the Frick Laboratory, namely, Mr. Morris F. Skinner for continued aid with stratigraphic information; Mr. Beryl Taylor for counsel and assistance; Messrs. Otto Simonis, Paul Geygan, and Ernest Heying, for the careful preparation of many of the specimens; Mr. George Krochak for assistance in the cataloguing and storage of the F:A.M. specimens; Miss Joan Connolly and Miss Iris Dowsey for assistance in typing; and Miss Kadge Hedlund for typing and preliminary editorial assistance. Staff members from the University of Nebraska State Museum provided valuable assistance, especially Prof. Mylan Stout for counsel concerning stratigraphic problems; Mr. Lloyd G. Tanner for field assistance and for his diligent checking of the field records; Mr. Henry Reider and Mr. Don Martin for preparation; Mr. Robert Eisele for the cataloguing and numbering of the leptauchenin specimens, and for aid in the preparation and proofing of the manuscript; Miss Elizabeth Rubendall, for editorial assistance and aid in bringing the manuscript to completion; Mrs. Norma Wagner for the typing and proofing of the manuscript; and Mrs. Linda Murphy and Mrs. Shirley M. Skinner for editorial assistance and typing of portions of the final manuscript.

Editorial Note

Mr. Charles H. Falkenbach died unexpectedly at Santa Fe, New Mexico, on June 8, 1962.

The research work on the oreodonts, as well as the preparation of the manuscript, had been virtually completed in the fall of 1961 at Lincoln, Nebraska. All the illustrations, including the preparation of the captions, had also been finished.

Between the years 1962 and 1967, when the report was submitted for publication, Dr. C. Bertrand Schultz has rechecked numerous specimens, listings, and geological data, and has been responsible for the final editing and arrangement of the manuscript.

Abbreviations

The institutions that contain oreodont remains referred to in the revision of the Mery-

[1] Schultz and Falkenbach, 1940, p. 216; 1941, p. 5; 1947, p. 165; 1949, p. 79; 1950, p. 95; 1954, p. 153; 1956, p. 381.

coidodontidae[1] are listed below, with the abbreviations used in the discussions and listings:

A.C., Amherst College
A.M., the American Museum of Natural History
A.N.S.P., Academy of Natural Sciences of Philadelphia
Aug. C., Augustana College, Rock Island, Illinois
B.E.G., U.T., Bureau of Economic Geology, University of Texas
C.I.T., California Institute of Technology (collections now deposited in the Los Angeles County Museum)
C.M., Carnegie Museum of Pittsburgh
C.N.H.M., Field Museum of Natural History (formerly Chicago Natural History Museum)
Col. M., Colorado Museum of Natural History
F:A.M., Frick Collection, or Frick American Mammals
F:B:A.M., Frick-Barbour Collection, Frick Laboratory and University of Nebraska State Museum

[1] Schultz and Falkenbach, 1940, 1941, 1947, 1949, 1950, 1954, and 1956.

K.U., University of Kansas Museum of Natural History
M.C.Z., Museum of Comparative Zoology, Harvard University
N.M., also U.S.N.M., United States National Museum, Smithsonian Institution
N.M.C., National Museum of Canada
N.S.M., also U.N.S.M., University of Nebraska State Museum
P.U., Princeton University
U.C., University of California Museum of Paleontology
U.M., University of Montana
U.N.S.M., also N.S.M., University of Nebraska State Museum
U.O., University of Oregon
U.S.N.M., also N.M., United States National Museum, Smithsonian Institution
S.D.S.M., South Dakota School of Mines
Y.P.M., Yale University, Peabody Museum of Natural History
W.M., Walker Museum, University of Chicago (collections now in the Field Museum of Natural History)
W.M.C.U., Woodwardian Museum, Cambridge, England

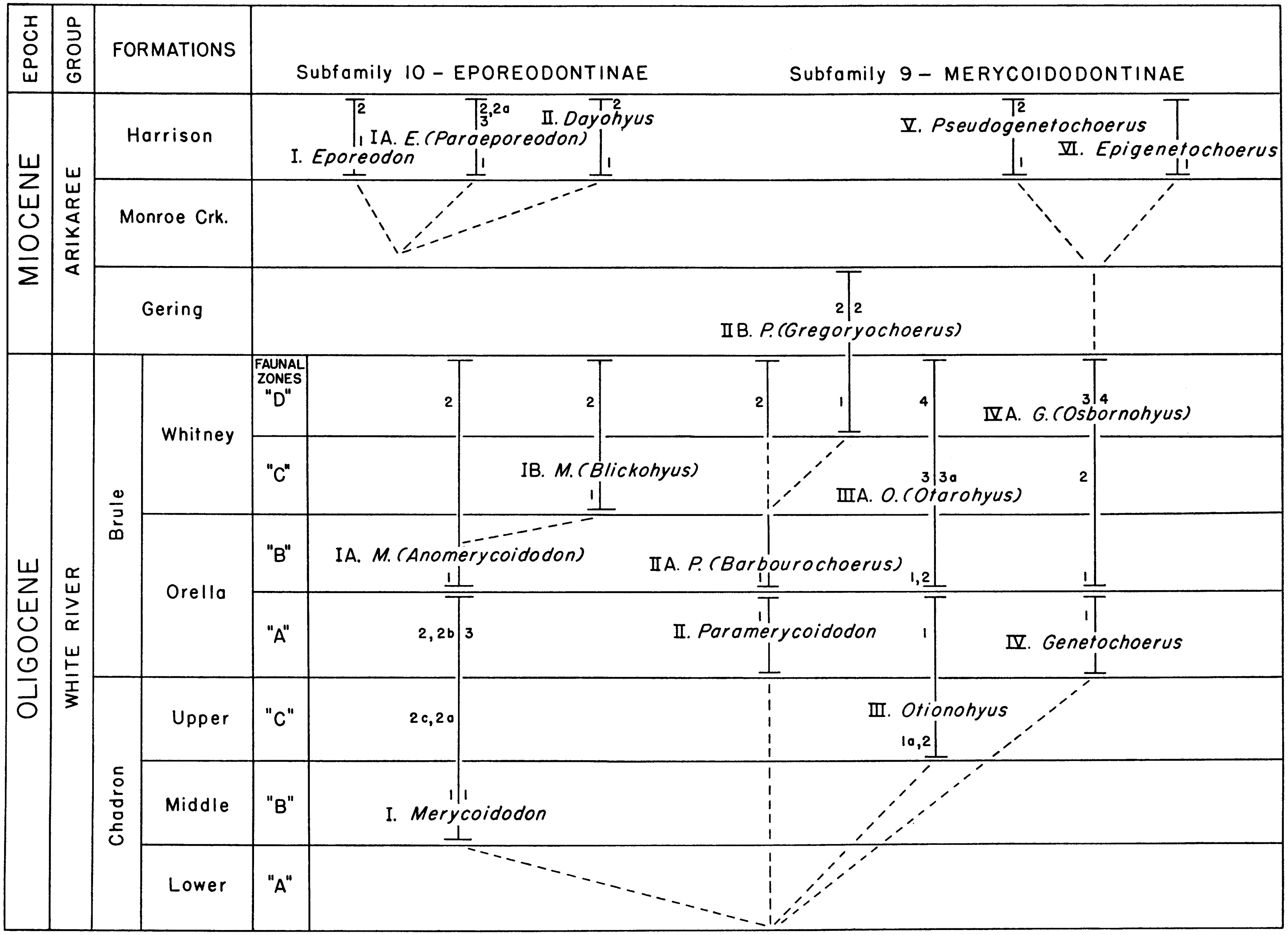

Chart 1. Stratigraphic distribution of the Merycoidodontinae and the Eporeodontinae.

EXPLANATION OF CHART 1: The use of faunal zones[1] in this report is continued to indicate approximate age equivalents of the occurrences in the various localities until definite geologic correlations can be established between the various Oligocene deposits in the Great Plains region.

The known geologic range of each genus and subgenus is indicated by a solid line with a horizontal bar at each end. Where a relationship between two phyla is questioned, the line is broken.

The numbers used here for species and subspecies are the same as those in the table of contents of this report. The numbers to the left of the vertical line indicate forms from the west-central Great Plains (Colorado, Nebraska, South Dakota, or Wyoming); those to the right, from localities outside this area (Montana, North Dakota, and Saskatchewan, Canada).

Subfamily 9. Merycoidodontinae

I. *Merycoidodon* Leidy
- 1. *M. forsythae,* new species
- 2. *M. culbertsonii* Leidy
  - 2a. *M. c. browni,* new subspecies
  - 2b. *M. c. osborni,* new subspecies
  - 2c. *M. c. osborni,* geologic variety
- 3. *M. macrorhinus* (Douglass)

IA. *Merycoidodon* (*Anomerycoidodon*), new subgenus
- 1. *M.* (*A.*) *dani,* new species
- 2. *M.* (*A.*) *lambi,* new species

IB. *Merycoidodon* (*Blickohyus*), new subgenus
- 1. *M.* (*B.*) *galushai,* new species
- 2. *M.* (*B.*) *lynchi,* new species

II. *Paramerycoidodon,* new genus
- 1. *P. georgei,* new species

IIA. *Paramerycoidodon* (*Barbourochoerus*), new subgenus
- 1. *P.* (*B.*) *bacai,* new species
- 2. *P.* (*B.*) *major* (Leidy)

IIB. *Paramerycoidodon* (*Gregoryochoerus*), new subgenus
- 1. *P.* (*G.*) *wanlessi,* new species
- 2. *P.* (*G.*) *meagherensis* (Koerner)

III. *Otionohyus,* new genus
- 1. *O. wardi,* new species
  - 1a. *O. wardi degrooti,* new subspecies
- 2. ?*O. vanderpooli,* new species

IIIA. *Otionohyus* (*Otarohyus*), new subgenus
- 1. *O.* (*O.*) *bullatus* Leidy
- 2. *O.* (*O.*) *cedrensis* (Matthew), Colo.
- 3. *O.* (*O.*) *hybridus* (Leidy)
  - 3a. *O.* (*O.*) *hybridus helenae* (Douglass)
- 4. *O.* (*O.*) *alexi,* new species

IV. *Genetochoerus,* new genus
- 1. *G. periculorum* (Cope)

IVA. *Genetochoerus* (*Osbornohyus*), new subgenus
- 1. *G.* (*O.*) *norbeckensis,* new species
- 2. *G.* (*O.*) *geygani,* new species
- 3. *G.* (*O.*) *chamberlaini,* new species
- 4. *G.* (*O.*) *dickinsonensis* (Douglass)

V. *Pseudogenetochoerus,* new genus
- 1. *P. covensis,* new species
- 2. *P. condoni* (Thorpe)

VI. *Epigenetochoerus,* new genus
- 1. *E. parvus* (Thorpe)

Subfamily 10. Eporeodontinae

I. *Eporeodon* Marsh
- 1. *E. occidentalis* Marsh
- 2. *E. davisi,* new species

IA. *Eporeodon* (*Paraeporeodon*), new subgenus
- 1. *E.* (*P.*) *longifrons* (Cope)
  - 1a. *E.* (*P.*) *l. perbullatus* (Thorpe)
- 2. *E.* (*P.*) *leptacanthus* (Cope)
- 3. *E.* (*P.*) *pacificus* (Cope)

II. *Dayohyus,* new genus
- 1. *D. trigonocephalus* (Cope)
- 2. *D. wortmani,* new species

[1] Falkenbach and Schultz, 1951, p. 47; Skinner, 1951, p. 57 (North Dakota section); also Schultz and Falkenbach, 1954, p. 153; 1956, p. 382. (See p. 423 for discussion of South Dakota geology.)

MERYCOIDODONTINAE Hay, 1902

Merycoidodontinae Hay, 1902, p. 665.
Merycoidodontinae Trouessart, 1905, p. 667.
Oreodontinae Gill, 1872, p. 81.
Oreodontiden Giebel, 1883, p. 132.
Oreodontides Cope, 1880d, p. 152.
Oreodonten Schlosser, 1890b, p. 722.
Oreodontes Winge, 1906, pp. 70, 134.
Cotylopinae Flower and Lydekker, 1891, p. 763.

Characters[1]

Skulls moderately small to medium in size; dolichocephalic to mesocephalic; low to moderately high; supraoccipital wings with moderate lateral spread (not fan-shaped as in Miniochoerinae[2]), extending posteriorly above and posterior to condyles; exoccipital foramen round to oblong; supraorbital foramina may be close together or distantly separated (most examples with prominent anterior grooves); anterior nasal-maxilla contact in area above posterior border of C/ to anterior border of P^1; orbits round to oblong; lacrimal fossa deep to shallow; nasals with slight anterior retraction, posterior border with much variation (acute, obtuse, or truncated); zygomatic arch with inward notch posterior to orbits; slight to prominent pit or depression on face above anterior premolars; bulla small (minute) to well inflated, with variation in depth of hyoidal groove (prominent in early geologic forms, lost in latest forms); postglenoid process compressed anteroposteriorly with varying degrees of robustness and inward slope of external borders; glenoid surface arched anteroposteriorly; palate projecting posteriorly to region of posterior border of M^3; noticeable increase in depth of ramus anteroposteriorly; inferior border of ramus approximately straight to a point below and posterior to M_3, then with a noticeable downward curve; ascending ramus moderately high, wide anteroposteriorly, posterior border with prominent robust rim or ridge to accommodate masseteric muscle; prominent apophysis or process below and posterior to condyle; apophysis light to moderately heavy, with external border higher and slightly more anterior than internal border; teeth brachyodont, $I\frac{1}{1}$–$I\frac{3}{3}$ increase in size; C/ and P_1 moderately large (no indication of large and small C/ and P_1 within a species as found in *Merychyus*); C/ long (vertically); /C incisiform; P_1 caniniform; external styles of M^1–M^3 well developed; molars with deep fossettes; crown surface from P^1–M^3 convex, P_2–M_3 concave (convex and concave surfaces similar to those found in examples of Miniochoerinae).

Discussion

Prior to 1956, the Merycoidodontinae (under the genus *Merycoidodon*) included small forms that have since been referred to the Miniochoerinae by Schultz and Falkenbach.[3] It was then noted and illustrated that the small forms that had been referred to the Merycoidodontinae differed from the true *Merycoidodon* species in that the skulls had fan-shaped postoccipital regions, thin enamel on the teeth, and shallow fossettes on the molars. The Miniochoerinae retained small (minute) bullae in the various phylogenetic lines. In the true *Merycoidodon* examples, however, the small (minute) bullae are restricted to the Chadron and "Zone A" of the Brule, but the bullae of *M.* (*Anomerycoidodon*) in zones "B," "C," and "D" of the Brule are well inflated.

Thorpe[4] retained the small forms under the genus *Merycoidodon* but made no attempt to divide the Merycoidodontidae into subfamilies. He did state, ". . . when he [Marsh] erected the genus *Eporeodon,* he emphasized the presence of the large bullae and the size of the skull, which is larger than that ordinarily seen in *Merycoidodon.*" The reference to the bullae is correct, but the size of the skull is not. (The genoholotype, *Eporeodon occidentalis,* is

[1] Compare with Schultz and Falkenbach, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85; 1950, p. 100; 1954, p. 163; 1956, p. 391; this report, pp. 33, 193, and 227.

[2] See detailed comparison of *Merycoidodon* and Miniochoerinae; Schultz and Falkenbach, 1956, p. 387.

[3] 1956, *M.* (*P.*) *affinis,* p. 405; *M.* (*P.*) *gracilis,* p. 413; *P. platycephalus,* p. 427; and *G. periculorum,* this report, p. 136.

[4] 1937, pp. 47, 56, 61, 63.

DISTINCTIVE CHARACTERS OF THE MERYCOIDODONTINAE[1]

	Skull	Sagittal Crest	Auditory Bulla	Dentition (All Brachyodont)	Anterior Intermediate Crest on Each of P^1–P^3
I. *Merycoidodon* (p. 33, figs. 1–3, 19–23, 51)	Medium size to moderately large, low to moderately high	Comparatively low	Small	Comparatively heavy	Weak to moderately strong
IA. *M.* (*Anomerycoidodon*) (p. 73, figs. 4–6, 19–23, 52)	Moderately large and high	Comparatively high	Large	Comparatively heavy	Weak
IB. *M.* (*Blickochoerus*) (p. 79, figs. 4–6, 19–23, 52)	Moderately large and high	Comparatively low	Large	Comparatively heavy	Weak to moderately strong
II. *Paramerycoidodon* (p. 86, figs. 6–9, 19–23, 52)	Moderately large and high	Comparatively high	Small	Comparatively massive	Strong
IIA. *P.* (*Barbourochoerus*) (p. 90, figs. 6–9, 19–23, 52)	Moderately large and high	Comparatively high	Large	Comparatively massive	Weak to moderately strong
IIB. *P.* (*Gregoryochoerus*) (p. 98, figs. 6–9, 19–23, 52)	Moderately large and high	Comparatively high	Large	Comparatively heavy	Weak to moderately strong
III. *Otionohyus* (p. 106, figs. 10, 11, 19–23, 52)	Medium size; moderately low	Comparatively low	Small	Comparatively heavy	Strong
IIIA. *O.* (*Otarohyus*) (p. 116, figs. 11–13, 19–23, 52)	Medium size; moderately high	Comparatively high	Large	Comparatively heavy	Strong
IV. *Genetochoerus* (p. 134, figs. 14–16, 19–23, 52)	Medium size; moderately high	Comparatively high	Small	Comparatively light	Strong
IVA. *G.* (*Osbornohyus*) (p. 142, figs. 14–16, 19–23, 52)	Medium size; moderately high	Comparatively high	Large	Comparatively light	Weak to moderately strong
V. *Pseudogenetochoerus* (p. 156, figs. 16, 17, 19–23, 52)	Moderately large and high	Comparatively medium high	Large	Comparatively light	Strong
VI. *Epigenetochoerus* (p. 164, figs. 18–23, 52)	Medium size; moderately high	Comparatively medium high	Large	Comparatively light	Weak

[1] Compare with Schultz and Falkenbach, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85; 1950, p. 100; 1954, p. 166; 1956, pp. 392, 454; present paper, pp. 198, 227.

smaller than examples of *Merycoidodon culbertsonii.*)

Simpson[1] believed that there was a stronger relationship between the two and stated, ". . . since *Eporeodon* is certainly close to *Merycoidodon,* I refer *Eporeodon* to it [Merycoidodontinae]." The present writers have failed to observe evidence that suggests that *Eporeodon* and *Merycoidodon* belong to the same subfamily. The phylogeny of the Merycoidodontinae is shown in chart 1 (p. 22) demonstrating the extinction of the subfamily in the late Oligocene, but with one possible survivor in the earliest Miocene (Gering).

The genoholotype of *Eporeodon* [*occidentalis*] was found in the John Day deposits, which are here considered as approximately equal in age to the Harrison[2] of the Great Plains. The skull of *E. occidentalis* is smaller than the latest geologically occurring examples of the Merycoidodontinae. The Eporeodontinae is an independent subfamily known only from the John Day deposits of Oregon.

The John Day genera *Pseudogenetochoerus* and *Epigenetochoerus* are questionably referred to the Merycoidodontinae. On page 194 of this report, the oreodonts of the John Day deposits are compared with those of the Great Plains formations.

Stratigraphic Distribution

Remains of the Merycoidodontinae have been recorded from the Chadron, Brule, and Gering formations (or deposits of approximately the same age) of Colorado, Montana, Nebraska, North Dakota, South Dakota, and Wyoming, and from the middle and upper John Day of Oregon. Examples of Eporeodontinae in contrast are known only from the middle and upper John Day deposits (approximately equal in age to the Harrison of the Great Plains) of Oregon. The leptauchenins are restricted to the Brule, Gering, and Monroe Creek formations (or deposits approximately equal in age) in California, Montana, South Dakota, and Wyoming. Noteworthy is the absence of leptauchenins from the Harrison of the Great Plains and from the John Day deposits of Oregon (see chart 16, p. 420). The same faunal zones as previously published by the present writers are used in all charts and throughout the present text.

Bump[3] named two units of the Brule of South Dakota and stated: "The unit formerly known as the *Oreodon* beds (Wortman), minus the upper *Oreodon* bed, is hereby designated the Scenic member. . . .

"This member [Scenic] is conveniently divided into two units; the lower and upper nodular zones . . . its lithology is remarkably uniform throughout the Big Badlands. This is also true of the upper nodular layer, and thus the Orellan-Whitneyan contact may be located without difficulty.

"The unit known as the *Protoceras* beds (*Leptauchenia* beds) is designated the Poleslide member. . . .

"This member may be subdivided into three units. The lower zone includes approximately 100 feet of rather barren clays. . . . The middle zone is that section where *Leptauchenia* nodules are developed. . . . The upper unit is composed of vertically weathered silty ash."

The correlation of the Orella and Whitney members of Nebraska with the faunal zones of Schultz and Falkenbach are shown in charts 1 and 13 (pp. 22 and 411). The oreodont faunal zones "A" and "B" of the Brule are equal to Bump's Scenic member, and faunal zones "C" and "D" to the Poleslide member. Bump did follow these correlations of Falkenbach and Schultz[4] and the published evidence of Schultz, Tanner, and Harvey,[5] and agreed that: (1) the "Upper *Oreodon* bed" is equivalent to the lower part of the Whitney and not the upper part of the Orella; (2) the much-discussed upper portion of the Sheep Mountain deposits is Miocene in age. He failed, however, to refer to these earlier correlations and conclusions. Schultz and Stout,[6] on the other hand, did not recognize that the "Upper *Oreodon* bed" was an equivalent of the lower part of the Whitney, when they proposed the names Orella and Whitney. The study of the Oligocene oreodonts was responsible for the revision in the correlation of the Nebraska and South Dakota geologic deposits and faunal zones. The oreodonts appear to be the first major group of fossil

[1] 1945, pp. 148, 264.
[2] Schultz and Falkenbach, 1949, chart 1, p. 80.
[3] 1956, p. 430.
[4] 1951, p. 49.
[5] 1955, p. 4.
[6] 1938, p. 1921.

mammals from the middle and upper Tertiary to be collected, studied, and reported upon from stratigraphic as well as morphologic standpoints.

Galbreath[1] discussed the various Oligocene deposits of Colorado and named several units. Clark,[2] in turn, published names for the various Chadron members of South Dakota, but neither the Colorado nor South Dakota beds have been definitely correlated with deposits of approximately the same age in other localities. In order to avoid confusion concerning geologic correlations, the oreodont faunal zones of Schultz and Falkenbach are used for the Oligocene in the text and charts of the present paper.

The faunal zones "A," "B," and "C" of the Chadron are based on the subdivisions of Osborn's[3] lower Tertiary faunal zone 17. Although Osborn considered the subdivisions as "geologic horizons," the present writers have treated these as faunal zones, similar to the ones of the Brule.

The University of Nebraska State Museum field parties have used the letters A, B, C, and D in the Orella and A, B, and C in the Whitney as stratigraphic collecting horizons in the Brule Formation.[4] These letters should not be confused with the oreodont faunal zones "A," "B," "C," and "D" of the Brule used by the present writers on their charts and throughout the text of the various reports on the oreodonts. The Chadron stratigraphic collecting horizons A, B, and C of Schultz and Stout, however, correspond in age to the oreodont faunal zones "A," "B," and "C" of the Chadron.

Characters in Auditory Bullae

The Merycoidodontinae include oreodonts possessing small (minute) to larger, well-inflated auditory bullae. The comparisons here are similar to those found in the Desmatochoerinae.[5] Thus, the bullae may be divided into three groups: (1) small[6] (minute) and slightly inflated as exemplified in *Merycoidodon* examples from the Chadron and "Zone A" of the Brule (similar to those of Miniochoerinae[7]); (2) large and inflated bullae with various degrees of grooving for the hyoid as in *M.* (*Anomerycoidodon*) *dani,* or any other forms of this subfamily from "Zone B" or "Zone C" of the Brule; and (3) large, inflated, and rounded, lacking (or almost so) groove for hyoid as in *P.* (*B.*) *major,* or any other forms of the Merycoidodontinae from "Zone D" of the Brule.

The present writers[8] have discussed the possible development of the auditory bulla from the small to large as is apparent in this subfamily. It should be noted that all oreodonts from "Zone A" of the Brule, with the exception of the leptauchenins,[9] possess small (minute) auditory bullae. In the leptauchenins the bullae are well inflated and are exceptionally large from "Zone A" of the Brule through the Monroe Creek Formation, whereas in the Miniochoerinae the bullae are small from "Zone C" of the Chadron through "Zone D" of the Brule.

The bullae of *Miniochoerus affinis* and *Merycoidodon culbertsonii,* both from "Zone A" of the Brule, are small in proportion to the sizes of the skulls of the two species. The bulla of the former is larger than that of the latter, but the skull of *M. culbertsonii* is at least two and one-half times the size of that of *M. affinis.*

In making sections of examples of various oreodont bullae, it has become obvious that the internal bone structure is not uniform. The structure of the oreodont bullae may be considered under four categories: (1) the thin-shelled bulla, internally hollow (in early Oligocene species); (2) the thick-shelled bulla, partially filled with bone tissue with the internal center open (early Miocene); (3) the thin-shelled, pyramid-shaped bulla (as in *Brachycrus*), internally filled with bone tissue (late Miocene); (4) the semi-depressed, thin-shelled bulla (as in *Ustatochoerus*), completely filled with bone tissue (Pliocene). Figure 55 illus-

[1] 1953. Also see present report, p. 405, for discussion of Wilson's 1960 report on Colorado.

[2] 1954, p. 197 (Ahearn, Crazy Johnson Butte, and Peanut Peak members of the Chadron Formation).

[3] 1929, p. 57. (See chart 13 and explanation, p. 412.)

[4] Schultz and Stout, 1955, p. 17. (See explanation of chart 13, p. 412 of the present report.)

[5] Schultz and Falkenbach, 1954, p. 155.

[6] The terms "small" and "large" refer to the actual size of the bulla, to differentiate between the sizes of the various bullae in each phylogenetic line.

[7] Schultz and Falkenbach, 1956, p. 384. The auditory bullae of the Miniochoerinae remained small throughout the geologic history of the subfamily.

[8] 1954, p. 155.

[9] P. 227, present report.

trates the cross sections as well as the internal views of the various examples of bullae.

Range of Variation

The apparent range of variation in the basal lengths of the skulls and in the superior and inferior dentitions within the Merycoidodontinae is shown in chart 2. The chart indicates a trend for the skulls to become larger within a phylogenetic line, as they occur progressively higher in the geologic scale. It will be noted that very little size change takes place in some lines between Brule "Zone A" and "Zone B," except that the auditory bulla is small (minute) in "Zone A" and becomes inflated in "Zone B." In zones "C" and "D," a greater inflation of the bullae is apparent.

A comparison of the basal lengths of the skull with the lengths of associated limb elements is presented in chart 3. There are not sufficient associated skeletal elements available to suggest definite trends. In examples of *P.* (*B.*) *major,* it is noteworthy that the skull has the longest basal length, and the cited percentages differ from those of other forms.

Proportion of Length of Limbs to Basal Lengths of Skulls

The limb elements of the Merycoidodontinae are not well represented in the collections. The proportions between length of limbs and basal length of associated skulls are presented in chart 3. The available measurements in the various forms are too few to indicate an overall aspect.

The Pollex in the Merycoidodontinae

The Merycoidodontinae is the second group of oreodonts in which a five-toed forefoot has been observed, and the Leptaucheniinae is the third. The first group noted in this revision to have retained a pollex was the Miniochoerinae.[1] Several excellent examples of metacarpal I have been preserved in examples of the latter subfamily. Remains of oreodonts with the five-toed manus have been obtained from deposits of the Chadron, "Zone A" of the Brule, and the Gering.[2] There has been no definite evidence of a hallux in any oreodonts.

[1] Schultz and Falkenbach, 1956, p. 364, fig. 9.

[2] For discussion of the pollex in the Leptaucheniinae from the Gering, see p. 232, present paper.

Comparisons of Merycoidodontinae and Miniochoerinae

The remains of the Merycoidodontinae indicate that the oreodonts of this subfamily were most abundant from late Chadron times through the Brule. A single species is also known from the Gering. This later form suggests a possible relationship to the Eporeodontinae from the John Day deposits of Oregon. The geologic history of the subfamily is similar to that of the Miniochoerinae, except the latter is not recorded from the Gering.

The major differences separating the Merycoidodontinae from the Miniochoerinae are: in the Merycoidodontinae (1) the fossettes of the molars are deep and are retained with much wear, whereas in the Miniochoerinae the fossettes are shallow and are lost with slight wear; (2) the enamel on the crowns of the molars is thick, in the Miniochoerinae the enamel is very thin; (3) the supraoccipital wings are produced posteriorly for a greater distance beyond the occipital condyles than in the Miniochoerinae; (4) the supraoccipital wings are moderately spread, but in the Miniochoerinae they are greatly spread and incorporated into a fan-shaped occipital region.[3]

Among the species that were considered referable to *Marycoidodon* prior to 1956[4] are: *Miniochoerus* (*Paraminiochoerus*) *affinis, M.* (*P.*) *gracilis, Platychoerus platycephalus,* and *Genetochoerus periculorum* (Cope), (p. 136, this report).

It is of interest that in the Miniochoerinae, the auditory bullae remained small (minute) throughout the geological history of the subfamily (oreodont faunal "Zone C" of the Chadron through "Zone D" of the Brule). In contrast, the auditory bullae of the leptauchenins[5] are well inflated throughout the recognized subfamily history ("Zone A" of Brule through Monroe Creek). In the Merycoidodontinae a greater morphologic change in the bullae is apparent. In the forms from faunal "Zone B" of the Chadron through "Zone A" of the Brule, the bullae are small, whereas in those from "Zone B" of the Brule or above, the bullae are inflated to different

[3] See Schultz and Falkenbach, 1956, p. 388, fig. 4.

[4] *Idem,* 1956, pp. 405, 413, and 427, respectively.

[5] Present report, p. 238.

degrees, reaching their maximum expansion in "Zone D" of the Brule.

A brief review of two reports dealing with several "species of Merycoidodon" is in order, so that the various forms involved can be better interpreted.

Boardman Bump and Fredric B. Loomis[1] published a study of the variation in the species of *Merycoidodon* which was based on "something over 100 skulls, most of them from one locality, near the head of Indian Creek, Niobrara Co., Wyoming." This would limit "most of them" to the "Zone A" of the Brule,[2] possibly with some from the upper part of the Chadron, and perhaps a few from higher deposits in the geologic sequence.

The examples in the collection were sorted by Bump and Loomis, who stated, "We found them distributed in the following proportions, typical at least of the locality we worked . . . *Merycoidodon gracilis*—12%; *M. affinis*—20%; *M. periculorum*—9.5%; and *M. culbertsonii*—58.5%."

Bump and Loomis further stated: "What we did find is expressed in figures 1 and 2, namely that *M. gracilis* and *M. periculorum* are markedly uniform assemblages, while *M. affinis* and *M. culbertsonii* have narrow, medium or wide headed varieties. Nor is the narrow, medium or wide type correlated with size, occurring in both longer and shorter skulls."

If it be granted that all the Bump and Loomis samples came from one faunal zone, those that they considered referable to *M. culbertsonii* might well be divided into the various species or subspecies here considered from deposits approximately equal in age to "Zone A" of the Brule. It is apparent that Bump and Loomis did not consider all factors involved in their studies, namely, morphologic characters, individual and sex variations, and precise stratigraphic occurrences.

In the second paper mentioned above, which involved an "Analysis of *Merycoidodon* skulls," Phleger and Putnam[3] also considered skulls of *M. culbertsonii*, *"M." periculorum*, *"M." gracilis*, and *"M." affinis* and concluded: "It is true also that the frequency curves constructed from the present measurement data are bimodal for the genus, strongly suggesting the existence of two *Merycoidodon* 'groups'—the *M. gracilis* 'group' and the *M. culbertsonii* 'group.' "

Schultz and Falkenbach[4] later referred both *gracilis* and *affinis* to the Miniochoerinae and considered the former as *Miniochoerus (Paraminiochoerus) gracilis* and the latter as *M. (P.) affinis*. The present writers have not examined all the specimens used by Bump and Loomis and by Phleger and Putnam, but it is evident that the smaller-sized skulls (of *gracilis* and *affinis*) with the fan-shaped occipital regions and the shallow fossettes of the molars are typical of the Miniochoerinae and differ generically from the larger skulls of the Merycoidodontinae, which have posteriorly produced supraoccipital wings, heavy enamel on the molars, and deep molar fossetes.[5]

The specimens referred to *"Merycoidodon"*

[1] 1930, p. 17, figs. 1-2.

[2] The Frick Laboratory collections made by Charles H. Falkenbach from the "head of Indian Creek" indicate that the deposits represent faunal "Zone A" of the Brule.

[3] 1942, p. 556.

[4] 1956, pp. 388, 390, 405, 413.

[5] Since the present paper was prepared, Miller and Wood (1963, pp. 707, 708) have reported on 12 specimens with milk teeth in the Amherst College Museum collection from "the middle Oligocene of South Dakota, Wyoming and Nebraska." These two workers wrote: "On the basis of milk teeth, then, there is no justification for recognizing more than two species [*gracilis* and *culbertsonii*], referable to a single genus [*Merycoidodon*], among these specimens. This of course, can not be interpreted as invalidating Schultz and Falkenbach's genus *Miniochoerus*, since the present study is limited to the upper milk teeth, but the milk teeth of *M. gracilis* are believed to give no basis for its recognition." Schultz believes that Miller and Wood did not consider all the available evidence when they suggested that *gracilis* belongs to the same genus (*Merycoidodon*) as *culbertsonii*. Both species had been evolving in separate phylogenetic lines, at least since late Eocene or earliest Oligocene times, and the adult examples of the two species have morphological characters that differ enough to place *gracilis* and *culbertsonii* in two different subfamilies. Perhaps the immature skulls reflect more of the common characters of their ancestors than do those of the adults. Certainly the two species did have ancestors in common if the phylogenetic lines are traced back far enough. On page 707 of their report, Miller and Wood did admit that "the details of the pattern [on the molars] are worn away much faster on the smaller specimens [*gracilis*] than on the larger ones [*culbertsonii*]. This, of course, is characteristic of the *Miniochoerinae* and helps to distinguish this subfamily from the Merycoidodontinae."

CHART 2

SIZE RANGE IN THE MERYCOIDODONTINAE[a]

	No. of Examples	Skull: Basal Length Range	Skull: Basal Length Mean	Dentition: P^1–M^3 Range	P^1–M^3 Mean	P_1–M_3 Range	P_1–M_3 Mean	M^3 AP[b] Range	M^3 AP Mean	M_3 AP Range	M_3 AP Mean
I. *Merycoidodon*											
M. forsythae, "Zone B" of Chadron (Wyo.)	6	160–169.5	164.5	79.5–81	80	81.5–88.5	85.5	17.5–20.5	19	22.5–23.5	23
M. culbertsonii, "Zone A" of Brule (Colo., Nebr., N. Dak., S. Dak., Wyo., Canada)	168	178–208	191	82–99	91	91–106	98	17–21.5	19	20.5–26	23.5
M. c. browni, "Zone C" of Chadron (Nebr., S. Dak., Wyo.)	15	185–192	188.5	83–97.5	89	94.5–101.5	99	17.5–21	19	21.5–25.5	23.5
M. c. osborni, "Zone A" of Brule (Colo., Nebr., N. Dak., S. Dak., Wyo.)	255	166–195	178	77–101	85.5	82.5–102.5	92.5	16–21	18	18.5–24.5	22
M. macrorhinus, "Zone A" of Brule (Mont.)	1	200	200	90.5	90.5	—	—	20	20	—	—
IA. *M.* (*Anomerycoidodon*)											
M. (*A.*) *dani*, "Zone B" of Brule (Nebr., N. Dak., S. Dak.)	16	190–195.5	192	88–92.5	91	94–102.5	98	18–21.5	19.5	23–25	24
M. (*A.*) *lambi*, "Zone D" of Brule (S. Dak.)	18	197–211	203.5	87–102.5	93	95.5–113.5	101.5	18–24	20.5	23–27	24
IB. *M.* (*Blickohyus*)											
M. (*B.*) *galushai*, "Zone C" of Brule (S. Dak.)	2	182	182	90.5	90.5	89	89	20	20	23.5	23.5
M. (*B.*) *lynchi*, "Zone D" of Brule (Colo., Nebr., S. Dak.)	28	185–205	196.5	86–99	93.5	100–113.5	106.5	17.5–25.5	21	23–29	24.5
II. *Paramerycoidodon*											
P. georgei, "Zone A" of Brule (Nebr., N. Dak., S. Dak., Wyo.)	38	183–207	196	88–100	93	91–108	99.5	18–21.5	19.5	20–29	24.5
IIA. *P.* (*Barbourochoerus*)											
P. (*B.*) *bacai*, "Zone B" of Brule (Nebr., S. Dak.)	3	197–199	198	92.5–97	94.5	—	—	19.5–26.5	22	—	—
P. (*B.*) *major*, "Zone D" of Brule (Nebr., S. Dak.)	55	205–234	217.5	104–111	99	99.5–116	109	20–24.5	22	24–28.5	26.5
IIB. *P.* (*Gregoryochoerus*)											
P. (*G.*) *wanlessi*, "Zone D" of Brule (Nebr., S. Dak.)	48	190–207	197	86.5–105	94	100–111.5	104	18–26	21.5	24–28	25.5
P. (*G.*) *meagherensis* = Gering (Nebr., Mont.)	3	202–210	206	95.5–99.5	97.5	100–106	103	18–21.5	19.5	—	—

CHART 2—(*Continued*)

	No. of Examples	SKULL		DENTITION							
		Basal Length		P^1–M^3		P_1–M_3		M^3 AP		M_3 AP	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
III. *Otionohyus*											
O. wardi, "Zone A" of Brule (Nebr., N. Dak., S. Dak., Wyo.)	102	155–176	165	74.5–85.5	80	81.5–90	86.5	14.5–18	16.5	19–22.5	21
O. wardi degrooti, "Zone C" of Chadron (Nebr., S. Dak., Wyo.)	5	164–164.5	164	78–80	79	88	88	18	18	20.5	20.5
?*O. vanderpooli*, "Zone C" of Chadron (Nebr.)	1	169	169	84.5	84.5	—	—	17	17	—	—
IIIA. *O.* (*Otarohyus*)											
O. (*O.*) *bullatus*, "Zone B" of Brule (Nebr., N. Dak., S. Dak.)	64	167–185	176.5	77–92	83	84–93.5	89	15–21	17.5	20–23	21
O. (*O.*) *cedrensis*, "Zone C" of Brule (Colo.)	6	170	170	81.5–86	83.5	—	—	18–21.5	20	24	24
O. (*O.*) *hybridus*, "Zone C" of Brule (Nebr., S. Dak.)	11	177–179	177	82.5–83.5	83	82.5–92	86.5	8.5–20.5	19	20–24	22.5
O. (*O.*) *alexi*, "Zone D" of Brule (Colo., S. Dak.)	29	188–205	194	81–95.5	89	93.5–105.5	100	17–23.5	19.5	21.5–25.5	24
IV. *Genetochoerus*											
G. periculorum, "Zone A" of Brule (Colo., Nebr., S. Dak., Wyo.)	44	153–173.5	161	71–85	77.5	76.5–88.5	84.5	14–17	16	17.5–22.5	19.5
IVA. *G.* (*Osbornohyus*)											
G. (*O.*) *norbeckensis*, "Zone B" of Brule (Nebr., N. Dak., S. Dak.)	12	163.5–168	165.5	74–79.5	77	82.5–85	83.5	15.5–16.5	16	18–21	20
G. (*O.*) *geygani*, "Zone C" of Brule (N. Dak., S. Dak.)	22	167–178	172.5	78.5–86	82.5	83–101.5	90.5	16.5–19	17.5	19–23.5	21.5
G. (*O.*) *chamberlaini*, "*Zone D*" *of* Brule (Nebr., S. Dak.)	17	175–180.5	177.5	76.5–84.5	80.5	93	93	17–21	18	21–24.5	23
G. (*O.*) *dickinsonensis*, "Zone D" of Brule (N. Dak.)	1	175	175	79.5	79.5	86.5	86.5	16.5	16.5	21	21
V. *Pseudogenetochoerus*											
P. condoni = Harrison (Oreg.)	26	179–189	184	80–90	84	100–100.5	100	17–19	18	25	25
P. covensis = Harrison (Oreg.)	25	190–197		82.5–91	87.5	90.5–100	95	17.5–20.5	18.5	21–23.5	23
VI. *Epigenetochoerus*											
E. parvus = Harrison (Oreg.)	5	160	160	70–73	71.5	77–79.5	78.5	16.5–17	16.5	19.5–20	19.5

[a] All measurements in millimeters.
[b] AP, anteroposterior.

CHART 3

PROPORTIONS OF LENGTHS OF LIMBS TO BASAL LENGTHS OF ASSOCIATED SKULLS IN THE MERYCOIDODONTINAE

	Skull, Basal Length (mm.)	Humerus B. L.	Radius B. L.	Ulna B. L.	Mc. III B. L.	Femur B. L.	Tibia B. L.	Mt. III B. L.
Merycoidodon culbertsonii								
A.M. 594	178	.74	.61	.82	.31	.85	.75	.37
F:A.M. 45159	199	—	—	—	—	.84	.72	.34
U.N.S.M. 28467	188	—	.60	.82	.30	—	.74	—
M. c. browni								
F:A.M. 72286	192	.73	.63	.84	.32	.86	.75	.37
M. c. osborni								
F:A.M. 49668	181	.78	.64	.88	.33	.90	.81	.33
A.M. 1287	178	.73	.64	.88	.32	.90	.80	.35
F:A.M. 72246A-B	192[a]	—	.59	.80	.31	.89	.77	—
F:A.M. 49644	(185)[b]	.74	.61	.76	.31	(.79)	—	.33
F:A.M. 49696	179	.77	.65	—	.32	(.97)	—	.40
M. (Anomerycoidodon) lambi								
F:A.M. 72139	201.5	—	.61	.85	.31	.86	.71	—
M. (Blickohyus) lynchi								
F:A.M. 72114	(185)	.77	—	—	—	.87	.76	.40
Paramerycoidodon georgei								
F:A.M. 72209	((190))	—	.77	.68	—	—	—	—
P. (Barbourochoerus) major								
F:A.M. 45298	222	.68	.56	.78	.26	.82	.68	—
Otionohyus wardi								
F:A.M. 49662	163	.76	.62	.84	—	—	.73	.38
F:A.M. 49654	175	—	.59	—	.30	—	—	—
O. w. degrooti								
F:A.M. 49760	164	.74	.63	.85	.31	.90	.79	—
O. (Otarohyus) bullatus								
F:A.M. 45267	((180))	.77	—	—	—	.88	.75	—
F:A.M. 45268	(178)	—	.65	—	—	—	.81	.40
Genetochoerus periculorum								
Y.P.M. 12565	165	(.77)	.64	.77	.31	—	—	.36
F:A.M. 49741	((165))	.78	.64	.87	—	—	—	—
F:A.M. 49730	158	.78	.67	.90	.32	.93	.81	.39
U.N.S.M. 28338	(156)	.74	.65	.89	—	—	—	—
G. (Osbornohyus) norbeckensis								
F:A.M. 49733	165	—	—	—	—	.87	.78	—

[a] Represents mean of two associated individuals, and the limbs may belong with either skull.
[b] ( ), Approximate; (( )), estimated.

periculorum in the reports by Bump and Loomis, and Phleger and Putnam, are here referred to *Genetochoerus periculorum* (Cope), page 136. The present writers have assumed that the identifications were correct. The examples of this species differ from those of *Merycoidodon culbertsonii* in having smaller-sized skulls and lighter dentitions. Both forms are from oreodont faunal "Zone A" of the Brule and possess small (minute) auditory bullae. Both species gave rise to forms that had inflated bullae (from faunal "Zone B" through "Zone D" of the Brule).

I. MERYCOIDODON Leidy

Merycoidodon Leidy, 1848, p. 47.

Merycoidodon (Oreodon) (Leidy): Loomis, 1924a, p. 369.

Merycodon Marschall, 1873, p. 333 (misprint for *Merycoidodon*).

Merychoidodon Lambe, 1908, p. 10 (misprint for *Merycoidodon*).

Oreodon Leidy, 1851a, p. 238. Cope, 1884a, p. 505 ("*Merycoidodon* syn. of *Oreodon*").

Oreodon (Merycoidodon) (Leidy): Barbour and Cook, 1917, p. 169.

Cotylops Leidy, 1851a, p. 239.

Cotylops (Oreodon) (Leidy): Nicholson and Lydekker, 1889, p. 1326.

Genotype: *Merycoidodon culbertsonii* Leidy.

Characters

Skull: Small size; basal lengths ranging from 160 to 208 mm., widths from 99 to 130 mm.; dolichocephalic; facial region moderately high; supraoccipital wings extending posteriorly for short distance beyond condyles, with lateral wings moderately spread (not fan-shaped as in Miniochoerinae); sagittal crest moderately high; brain case long and narrow; frontal wide (not reduced as in Desmatochoerinae); nasals light to moderately heavy, with considerable individual variation, especially in width; posterior border of nasals acute, obtuse, or truncated; nasal-maxilla anterior contact in area above posterior portion of C/; supraorbital foramen from near to comparatively distant from midline of skull; orbits semiround and of medium size, looking outward, forward, and slightly upward; malar shallow (deeper in examples of *M. macrorhinus*) below orbit, inferior border with sharp upward curve posteriorly; zygomatic arch moderately light; lacrimal fossa moderately deep [more so than in examples of *M.* (*Anomerycoidodon*), decidedly less depth than those of Eporeodontinae], oval to round; infraorbital foramen in area above P^3; muzzle slightly inflated; premaxillae not fused; occipital condyles moderately light; paroccipital process moderately light, anterior-external area excavated; bulla small (minute) [differing from the well-inflated bulla of examples of *M.* (*Anomerycoidodon*)], similar to all oreodonts from "Zone C" of Chadron or "Zone A" of Brule, except inflated ones of Leptaucheniinae from latter zone; postglenoid process from moderately light to semirobust, wider transversely than anteroposteriorly, external border sloping down and inward, comparatively long vertically (considerable individual variation).

Mandible: Moderately light; postsymphysis in area below P_3-P_4; ramus moderately deep; inferior border of ascending ramus with inward curve (less noticeable in other lines of subfamily); condyle moderately large (lighter than in examples of *Paramerycoidodon*).

Dentition: Light (lighter than examples of *Paramerycoidodon* and its subgenera, heavier than those of *Genetochoerus* and *Otionohyus* and their subgenera); C/ long and more or less robust; P^1–P^3 each with weak to prominent anterior intermediate crest.

Limbs: Moderately long and somewhat heavy, longer than examples of Miniochoerinae. (Examples with five digits on forefoot.)

Measurements: Tables 1 and 7 (pp. 35 and 146).

Illustrations: Figure 1–3, 51 (skulls, mandibles, and dentitions), 19–23 (limb elements).

Discussion

The genus *Merycoidodon* was the first published name of the large and diversified Merycoidodontidae. Leidy's[1] original material was fragmentary and did not represent a mature individual. Later he[2] named two new genera, *Oreodon* and *Cotylops*, also based on fragments. Still later Leidy,[3] with the aid of additional material, rightly concluded that *Mery-*

[1] 1848, p. 47.

[2] 1851a, p. 238, *Oreodon priscum* (see p. 39 for specific synonym); 1851a, p. 239, *Cotylops speciosa* (see p. 39 for specific synonym).

[3] 1852a, p. 540.

coidodon, Oreodon, and *Cotylops* were synonyms but unfortunately preferred to retain the name *Oreodon* in preference to the first-named *Merycoidodon.* To support his decision Leidy stated, ". . . for which I propose to retain the name *Oreodon* as being less exceptionable than that of *Merycoidodon.*"

The genus *Merycoidodon* has priority. Cope,[1] however, also rejected *Merycoidodon* and used *Oreodon.* Hay,[2] in discussing the genus, stated, "Professor Cope has rejected the name [*Merycoidodon*] on the ground that it is a *nomen nudum;* but a generic name is hardly *nudum* when it is supported by a well-defined species and is moreover, clothed with two pages of description." Douglass[3] and Thorpe[4] also agreed that *Merycoidodon* had priority over *Oreodon.*

In a discussion of the generic characters of *Oreodon* (=*Merycoidodon*), Cope[5] reported: "The cranial characters which belong to *Oreodon* as a genus are the following: Orbit complete behind. Temporal fossa separated by a sagittal crest. A lachrymal fossa, but no facial nor frontal vacuities. Premaxillary bones distinct from each other and from the maxillaries. Nasal bones well developed. Auditory bullae not inflated." He further recommended ". . . the removal [from *Oreodon*] of the forms with inflated bullae to the genus *Eucrotaphus.*"

Cope's conclusions were similar to those of the present writers, i.e., in a single subgeneric line forms with inflated bullae are subgenerically different from those with small (minute) bullae. In all phyla of the oreodonts in the present revision, those species having minute bullae are considered as belonging to a genus, and forms derived from them and having inflated bullae are referred to a subgenus in the same phylogenetic line.

All previous authors have accepted the genotypic species of *Merycoidodon* as *M. culbertsonii,* which is based on fragments of an immature maxilla and mandibular ramus. Also, all have considered the type as coming from the lower Brule ("Zone A"). Later, additional specimens by various writers were referred to this genus and species, and those skulls that had the bullae preserved exhibited small (minute) ones.

The present writers also consider that the immature material represents the holotype of the genotypic species, but wish to note that it is possible that the cotypes may be identified as examples of *M. culbertsonii osborni* from "Zone A" of the Brule, or *M.* (*Anomerycoidodon*) *dani,* or *Otionohyus* (*Otarohyus*) *bullatus.* The last two mentioned species are from "Zone B" of the Brule and possess inflated bullae. With an identification based on dentition alone, it seems impossible to separate these forms.

The proposed evolutionary sequence of the species of *Merycoidodon* is as follows: *M. forsythae* from "Zone B" of the Chadron, *M. culbertsonii browni* from "Zone C" of the Chadron, and *M. culbertsonii* from "Zone A" of the Brule. In addition there are two forms not considered in the direct phylum but as closely associated lineages: *M. c. osborni* from "Zone A" of the Brule (including a geologic variety of this subspecies from "Zone C" of the Chadron) and *M. macrorhinus* from "Zone A" of the Brule.

Distribution

Three species and two subspecies of *Merycoidodon* are here recorded from the lower and middle Oligocene (zones "B" and "C" of the Chadron and "Zone A" of Brule) of Colorado, Montana, Nebraska, North Dakota, South Dakota, and Wyoming; also Saskatchewan, Canada. (See geological distribution chart, p. 22.)

Summary of Species and Types

Three species, two subspecies, and a geologic variety of *Merycoidodon* from 17 Oligocene localities are here recorded:

1. *Merycoidodon forsythae,* new species, from Natrona County, Wyoming; referred remains from Jefferson County, Montana; and tentatively referred from Saskatchewan, Canada. (Oreodont faunal "Zone B" of Chadron.)

Holotype: Skull, F:A.M. 72303. Figures 1, 2, 51.

2. *Merycoidodon culbertsonii* Leidy, from South Dakota; referred remains from Shannon, Pennington, Washabaugh, Jackson, and Harding counties, South Dakota; Sioux,

[1] 1884a, p. 505.
[2] 1899, p. 594.
[3] 1906, p. 565.
[4] 1937, p. 23.
[5] 1884a, pp. 506–511.

TABLE 1

Merycoidodon Leidy. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*M. forsythae*, new species	*M. culbertsonii*, Leidy		*M. c. browni*, new subspecies	*M. c. osborni*, new subspecies	*M. c. osborni*, geol. variety	*M. macrorhinus* (Douglass)
	Holotype F:A.M. 72303	Cotypes A.N.S.P. 10728	Referred F:A.M. 45155	Holotype F:A.M. 72286	Holotype F:A.M. 49668	Example U.N.S.M. 28200	Holotype C.M. 767
Stage of wear of teeth	(w‡)	(−M)	(w‡)	(w)	(w+)	(w‡+)	(w)
Length (incl. supraoccipital crest and incisors)	((180))	—	215	222	211.5	((200))	((230))
Basal length (from anterior notch of foramen magnum to posterior base of I¹)	165	—	190	192	181	((178))	((200))
Width (max.)		—	115	100.5	115	((119))	((125))
Width of brain case (max.)	(50)	—	53	57	61	64.5	—
Width, interorbital (min.)	49	—	61	56	49	(64)	((67))
Distance from anterior rim of orbit to anterior base of C/	69	—	86	79	76	(75)	(88.5)
Distance from anterior rim of orbit to supraoccipital crest	(115)	—	131	137.5	134.5	—	—
Length of nasals	—	—	81	81.5	(80)	—	((96))
Width of muzzle at infraorbital foramina	45.5	—	54	37	51	54	59
Width across canines	((32))	—	47.5	44.5	(45)	—	(53)
Length, C/−M³ incl.	94	—	103	102	101	—	107
Length, P¹–M³ incl.	85	—	90.5	90	89	86.5	90.5
Length, P¹–P⁴ incl.	39	—	45.5	44.5	44.5	43.5	45
Length, M¹–M³ incl.	48.5	—	46.5	47	47	45.5	47.5
Length, M²	—	(15.5)	15	18.5	18	16.5	17
Length, M³	20.5	19.5	19.5	20	18	19.5	19
Width of M³ (max.)	19.5	17	19	19	18	19	20
Depth of malar below orbit	14	—	17	18	15.5	16.5	21
MANDIBULAR RAMUS	Referred F:A.M. 72308	A.N.S.P. 10727					
Stage of wear of teeth	(M)	(−M)	—	—	—	—	—
Length (max., incl. incisors)	(140)	—	176	173.5	165	—	—
Length, /C, condyle incl.	(128)	—	161.5	160.5	150.5	—	—
Depth of jaw under coronoid	66.5	—	83	(76)	—	—	
Depth of jaw below anterior edge of M₃	31.5	—	37	34	37.5	39.5	—
Length, /C–M₃ incl.	89.5	—	109.5	109	102.5	—	—
Length, P₁–M₃ incl.	86	—	97	99	96.5	(90)	—
Length, P₁–P₄ incl.	35.5	—	45.5	46.5	44	(41)	—
Length, M₁–M₃ incl.	50.5	((53))	51.5	52	52	49	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

Dawes, and Scotts Bluff counties, Nebraska; Niobrara and Converse counties, Wyoming; Stark County, North Dakota; and Colorado. ("Zone A" of Brule.)

HOLOTYPE: Maxilla and ramus, A.N.S.P. 10727 and 10728 (? one individual). Figure 3.

2a. *Merycoidodon culbertsonii browni*, new subspecies, from Niobrara County, Wyoming; referred remains from Converse County, Wyoming; Dawes and Sioux counties, Nebraska; and Shannon County, South Dakota. ("Zone C" of Chadron.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 72286. Figures 1–3, 19–23.

2b. *Merycoidodon culbertsonii osborni*, new subspecies, from Shannon County, South Dakota; referred remains from Shannon, Pennington, Jackson, and Harding counties, South Dakota; Sioux and Scotts Bluff counties, Nebraska; Converse and Niobrara counties, Wyoming; Stark County, North Dakota; and Logan County, Colorado. ("Zone A" of Brule.)

2c. Geologic variety from Sioux and Dawes counties, Nebraska; and Niobrara County, Wyoming. ("Zone C" of Chadron.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 49668. Figures 1–3, 19–23.

3. *Merycoidodon macrorhinus* (Douglass), from Broadwater County, Montana. ("Zone A" of Brule.)

HOLOTYPE: Partial skull, C.M. 767. Figures 1, 3.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MERYCOIDODON

TOTAL AVAILABLE SPECIMENS: 443[1]

1. Merycoidodon forsythae,[2] new species

From "Zone B" of the Chadron Formation, Bates Hole, Natrona County, Wyoming; referred from Jefferson County, Montana; and tentatively referred from Saskatchewan, Canada

DESCRIPTION

SKULL: Smallest of genus; sagittal crest lower than in type of *M. culbertsonii browni;* frontal narrower transversely than in other examples of genus; nasals lightest of genus, posterior border acute; orbit round, smallest of genus, directed mostly outward and slightly upward; malar below orbit shallowest of genus; lacrimal fossa oval in outline, others of genus more rounded; postglenoid process not so long vertically as in examples of *M. c. browni.* (See generic characters.)

MANDIBLE: Same size comparisons as skull. (See generic description.)

DENTITION: Series of less length than other examples of genus; premolars more crowded than usual in this genus; C/ lighter than usual in this genus; P^2–P^3 each with extremely noticeable anterior intermediate crest (P^1 incomplete in available material). (See generic characters.)

LIMBS: Short and moderately light (shortest and lightest of genus); approaching size of examples of *Genetochoerus.*

MEASUREMENTS: Tables 1 and 7 (pp. 35 and 146).

ILLUSTRATIONS: Figures 1–3, 19–23, 51.

DISCUSSION

The new species, *Merycoidodon forsythae*, is represented by the best-preserved skull of the genus from "Zone B" of the Chadron available to the writers. The holotype appears to represent a form similar to that of *Merycoidodon culbertsonii browni* from "Zone C" of the Chadron but of smaller size. As noted in many of the Chadron oreodonts, the dentition is large for the size of the skull, which indicates that the teeth increased in size at a more rapid rate than did the skull. The outstanding dental character is the extremely robust anterior intermediate crest on P^1–P^3. P^1 is broken in the holotype, but presumably it was comparable with P^2–P^3 in this respect.

The remains of this new species suggest that this form was the ancestral stock from which *M. c. browni* from "Zone C" of the Chadron developed. The size difference between skulls of *M. forsythae* from "Zone B" of the Chadron and those of *M. c. browni* from "Zone C" of the Chadron suggests that more time elapsed between Chadron zones "B" and "C" than between Chadron "Zone C" and Brule "Zone A" (the faunal zone for *M. culbertsonii*). Other

[1] Includes 348 F:A.M. and 52 U.N.S.M. specimens.

[2] Named in honor of Miss Ellen Forsythe, artist of the Frick Laboratory, who has drawn many of the oreodont examples.

oreodont phyla indicate that there was not a noticeable faunal break between the Chadron and Brule formations. The geologic evidence appears to agree with the paleontologic observations, since there is not an unconformity between the Chadron and the Brule.

The Oreonetinae[1] include oreodont forms from "Zone B" of the Chadron, but do not appear to be ancestral to oreodonts from later deposits, except perhaps to the Leptaucheniinae. In both *Oreonetes* and *Limnenetes,* the bullae are greatly inflated, actually to the degree found in oreodonts from "Zone D" of the Brule. In *M. forsythae,* however, the bullae are small (minute) and comparable with those of *Merycoidodon culbertsonii.*

Three specimens from the Pipestone Springs area of Montana are fragmentary but suggest this same species. The Bates Hole, Wyoming, and Montana localities are here considered to be approximately equal in age. Both localities have yielded examples of *Bathygenys alpha.*[2]

Fourteen specimens are here recorded:

HOLOTYPE

Skull with I^1–P^1 br.[3] and P^2–M^3. (w‡)[4]	F:A.M. 72303	From oreodont faunal "Zone B" of Chadron Formation, 65′ above Black Camel Ash, [D+65′],[5] 6 mi. N. and 1½ mi. W. of Alcova, Bates Hole, Natrona County, Wyoming; collected by Morris Skinner, Ted Galusha, and associates, 1957 Figures 1, 2, 51

REFERRED FROM (A) NATRONA COUNTY, WYOMING; (B) JEFFERSON COUNTY, MONTANA; AND (C) TENTATIVELY REFERRED FROM SASKATCHEWAN, CANADA

A. FROM BATES HOLE, NATRONA COUNTY, WYOMING (COLLECTED BY MORRIS SKINNER, TED GALUSHA, AND PARTY, 1957–1958)

From 6 Mi. N. and 1½ Mi. W. of Alcova:

SKULL AND MANDIBLE		F:A.M.
Partial skull with C/–M^3 br. and partial mandible with I_2–P_1 rt. and P_2–M_3 (P_2–P_3 br.) Figure 3 [D–15′]	(M)	72308

From 6 Mi. N.W. of Alcova:

MANDIBULAR RAMUS		
Partial left ramus with P_2–M_3 br.	(w‡)	72293

From 7–8 Mi. S.E. of Alcova:

MANDIBULAR RAMUS AND SKELETAL ELEMENTS		
Mandibular ramus with I_2 alv. and /C–P_4 rt. and M_1 (br.)–M_3, 2 partial humeri, 2 ulnae and radii, 2 partial manus, 2 femora (1 partial), 2 tibiae, astragalus, calcaneum, partial pes, vertebrae, and ribs. Figures 19–23 [G–15′]	(w+)	72325

From 2–2½ Mi. W. and 4 to 4½ Mi. N. of Alcova:

[1] Schultz and Falkenbach, 1956, p. 453.
[2] Schultz and Falkenbach, 1956, p. 465, and p. 383, this report.
[3] Abbreviations used in descriptions: alv., alveolus or alveoli; br., broken; erupt., erupting; rt., root or roots.
[4] Stage of wear of teeth: (I), immature; (M), mature; (W), worn.
[5] See footnote 1, p. 383.

SKULL AND MANDIBULAR RAMI

Anterior portion of skull with P^1–M^3 rt. and left ramus with I_2 alv. and I_3–M_3 rt. [G–35′]		F:A.M. 72321

MAXILLA AND MANDIBLE

Partial left maxilla with P^4–M^3 br. and partial mandible with I_3–P_1(br.) and P_2–M_3 [G–20′]	(w‡+)	72322

SKULL

Partial skull with C/–P^1 rt. and P^2(br.)–M^3(br.) [G–30′]	(w)	72323

MANDIBULAR RAMUS

Partial left ramus with P_2–P_3 alv. and P_4–M_3 [G+35′]	(M+)	72324

B. FROM PIPESTONE SPRINGS, JEFFERSON COUNTY, MONTANA (COLLECTED BY CHARLES H. FALKENBACH AND PARTY 1942 AND 1934)

MAXILLA

		F:A.M.
Partial right maxilla with P^4(br.)–M^3(br.) (M^2 rt.)	(w‡)	72301

2 MANDIBULAR RAMI

Partial left ramus with P_2(rt.)–M_1	(w‡)	72294
Partial left ramus with P_3	(w+)	72295

TENTATIVELY REFERRED FROM OLIGOCENE DEPOSITS, CYPRESS HILLS, SASKATCHEWAN, CANADA

(COLLECTED BY WESTON, 1884, AND LAMBE, 1904)

DISASSOCIATED TEETH

		N.M.C.
Left C/.	Figured by Lambe, 1908, pl. 2, figs. 20–23	
Left /C.		6272
Left P_1.	Figured by Lambe, 1908, pl. 2, figs. 18–19	to
Right M_2.	Figured by Lambe, 1908, pl. 2, figs. 24–26	6274

The present writers have not seen the above disassociated teeth, but, from the evidence shown on Lambe's illustrations, they doubt if the actual specimens can be identified with any degree of accuracy. Lambe[1] identified the above specimens as "*Merychoidodon*[2] *culbertsonii,*" but they are here tentatively referred to *M. forsythae.*

2. **Merycoidodon culbertsonii**[3] Leidy

From oreodont faunal "Zone A" of the Brule Formation, South Dakota; referred remains from Shannon, Pennington, Washabaugh, Jackson, and Harding counties, South Dakota; Sioux, Dawes, and Scotts Bluff counties, Nebraska; Niobrara and Converse counties, Wyoming; Stark County, North Dakota; and Logan County, Colorado

Merycoidodon culbertsonii LEIDY, 1848, p. 47, figs. 1–5. LAMBE, 1908, pl. 2, figs. 18–26. OSBORN, 1910, p. 218, fig. 106. STROMER, 1912, p. 199, fig. 182. SCOTT, 1913, figs. 136, 202, 204A; 1940, p. 669, pls. 69–70. THORPE, 1923a, p. 225, fig. 1; 1923b, p. 91, figs. 5–6; 1937, p. 47, figs. 3, 7, 21–23, pl. 2, figs. 3–6, pl. 40. LOOMIS, 1924b, p. 2, figs. 1–4; 1925c, p. 586, fig. 1. WEBER AND ABEL, 1928, p. 612, fig. 408.

Merycoidodon culbertsonii culbertsonii (Leidy): THORPE, 1921f, p. 334.

Merychoidodon culbertsoni (Leidy): LAMBE, 1908, p. 10. (See *M. forsythae,* the present report, p. 36.)

Oreodon culbertsonii LEIDY, 1852a, p. 548, pl. 13, figs. 3–4; 1854a, pl. 2, figs. 1–4, pl. 3, pl. 4, figs. 3–4, pl. 5, figs. 1–2, pl. 6, figs. 8–11; 1869, p. 86, pl. 6, fig. 1, pl. 7, fig. 2, pl. 9, fig. 1. GAUDRY, 1878, p. 81, fig. 90. GIEBEL, 1883, pl. 44. SCOTT, 1890b, figs. 2–4, 10, pl. 12, pl. 13, fig. 4 (not this genus and species), pl. 16, figs. 27–29. OSBORN

[1] 1908, p. 10, pl. 2, figs. 18-26.
[2] Misprint for *Merycoidodon.*
[3] The specific name *culbertsonii* was originally spelled by Leidy (1848, p. 47) with two "i" 's, but many later writers, including Leidy himself at a later date, have used a single "i."

AND WORTMAN, 1894, p. 215, fig. 5a. STEWART, 1897, p. 13, pl. 1. WEBER, 1904, p. 663, fig. 476. O'HARRA, 1920, p. 128, pl. 21, fig. B, pl. 24, fig. B, pl. 40.[1] ZITTEL AND SCHLOSSER, 1911, p. 483, figs. 673–674; 1923, p. 572, figs. 714–715. MOODIE, 1915, p. 174, fig. 14. BARBOUR AND COOK, 1917, p. 165, figs. 4, 6. GREGORY, 1920, p. 188, fig. 156. ABEL, 1926, figs. 214, 228.

Oreodon priscum LEIDY, 1851a, p. 238. (Milk teeth, according to Thorpe, 1937, p. 47.)

Cotylops speciosa LEIDY, 1851a, p. 239.

Oreodon priscus LEIDY, 1851b, p. 276.

Oreodon robustum LEIDY, 1851b, p. 276.

Oreodon (*Merycoidodon*) *culbertsonii* (Leidy): O'HARRA, 1910, p. 109, pl. 43, fig. 2.

CHARACTERS

SKULL: Considerable individual variation in length and width (wider skulls perhaps represent male examples); brain case usually long and narrow, more so than in *M. c. osborni;* tendency for longer face (C/ to orbit) than in mentioned subspecies; nasals with acute, obtuse, or truncated posterior border; postglenoid process varying in degree of robustness (not so robust as in examples of *Paramerycoidodon dani* from same faunal zone); muzzle narrower than in holotype of *M. macrorhinus.* (See generic characters.)

MANDIBLE: Inferior border of ascending ramus with marked inward curve, more so than in examples of *M. c. osborni.* (See generic characters.)

DENTITION: Weak anterior intermediate crest on P^1–P^3 inclusive, weaker on average than in examples of *M. c. osborni;* P^3 with weaker anterior intermediate crest than in holotype of *M. macrorhinus* (P^3 only complete premolar preserved in holotype of latter). (See generic characters.)

LIMBS: (See generic characters.)

MEASUREMENTS: Tables 1 and 7 (pp. 35 and 146).

ILLUSTRATIONS: Figures 1–3, 19–23, 51.

DISCUSSION

Leidy named *Oreodon priscum*[2] and *Cotylops speciosa*[3] and later[4] he came to the correct conclusion that both species were synonymous with *Merycoidodon culbertsonii* (see discussion, p. 38). He also illustrated a skull (pl. 10, fig. 4),[5] which is here considered as referable to *M. culbertsonii,* and a second skull and mandible (pl. 10, figs. 5 and 6, U.S.N.M. 137) here referred to *Genetochoerus periculorum* (Cope), page 136. Leidy[6] also used the name *Oreodon robustum* which apparently was a *lapsus calami* for *O. priscum,* as indicated by Leidy's statement, "Dr. Leidy presented for the inspection of the members a mutilated cranium . . . [using] the name of *Oreodon robustum.**" The footnote was "Proc. Acad. Nat. Sci., 5, p. 238," which is the original reference of *O. priscum.*

The assemblage of specimens here referred to *Merycoidodon culbertsonii,* all from "Zone A" of the Brule, shows a considerable amount of individual variation, especially in the width of the skulls, the shape of the posterior border of the nasals, and the postglenoid process. The material actually demonstrates more individual variation than does any other species from the Brule. It perhaps represents a time in the history of the phylum when rapid character transitions were taking place.

Leidy,[6] as more material was collected and identified, added to his original characters of *M. culbertsonii.* He noted that the nasals of *M. culbertsonii* showed considerable variation and stated: "The nasal bones of *Oreodon culbertsonii* vary in their proportionate breadth and transverse convexity in different skulls. Usually the posterior extremities together form an acute isosceles triangle between the anterior angular process of the frontals. The triangle varies in length, and degree of acuteness. The sides are more or less slightly convex, especially towards the base. In a few instances the apex is observed to be more or less rounded, and rarely notched." Of the 110 specimens examined by the present writers, 28 have obtuse (plus or minus) posterior borders of the nasals, and 82 possess acute borders.

Leidy also suggested that a certain narrow skull that was less robust and with smaller canine teeth than other examples was ". . . suspected to have belonged to the female."

The present writers agree with Leidy's con-

[1] In the text O'Harra recognized the genus *Oreodon,* but in the plate captions he considered it as a subgenus of *Merycoidodon.*

[2] 1851a, p. 238.

[3] 1851a, p. 239.

[4] 1852a, p. 540.

[5] 1851b, p. 276.

[6] 1869, pp. 80, 87.

clusion as to the great amount of individual variation in the nasals and that there are both light and robust skulls, which may indicate sexual variation. It is questionable if all of Leidy's referred material actually is *M. culbertsonii,* or if all of it came from the "Zone A" of the Brule.

The examples of *M. culbertsonii* include individuals that had five digits on the forefoot. The Miniochoerinae[1] also had five digits in the forefoot.

Sinclair[2] reported, ". . . there is a specimen of *O. culbertsonii* in our Museum [P. U.], No. 11080, labeled in Hatcher's handwriting as from the Upper *Oreodon* beds ["Zone C" of Brule], Corral Draw, and in a matrix which agrees in character with the Upper *Oreodon* clays."

Sinclair (p. 102), however, showed 32 specimens of *Merycoidodon culbertsonii* collected during 1920–1922, all from "Lower Nodular Zone" (= "Zone A" of Brule).

All the recognized examples of *M. culbertsonii* in both the Frick Laboratory and the University of Nebraska State Museum have field data showing their occurrence as "Zone A" of the Brule. In many instances, if specimens from the upper part of the Brule lack the bulla, it is very difficult to place the form correctly in the phylogenetic series except on its geological occurrence.

Scott[3] also referred two specimens, P. U. 11441 and 12764, to *Merycoidodon culbertsonii.* The present writers[4] have referred the former to *Desmatochoerus shannonensis,* and the latter to *Merycoidodon c. browni* (p. 55).

In a discussion of occurrences of oreodonts from the John Day deposits, Thorpe[5] reported: "Leidy, in 1870, identified some John Day specimens with his *M. culbertsonii,* but three years later he suspected that this material probably belonged to *Eporeodon bullatus.* There are a few isolated fragments of maxillae and rami which are almost identical with the corresponding parts of *M. culbertsonii,* but, in the absence of complete skulls, I hesitate to state definitely that this species occurs in the John Day Basin, although I rather believe it does." Independently Leidy and Thorpe actually were comparing material from the lower Miocene (Harrison equivalent) with specimens from the middle Oligocene ("Zone A" of the Brule). The present writers consider that the deposits of the middle and upper John Day Basin are approximately equal in age to the Harrison of the Great Plains and are not equivalent to the Oligocene.[6]

There are maxillae and rami of John Day forms that compare favorably with examples of *M. culbertsonii.* In fact, they may also compare superficially with examples of other genera and species of oreodonts from the Great Plains representing various geological ages. It should be noted, however, that teeth alone are not always sufficient for identification. Accurate identification can always be made much more readily when exact geologic data are available for the specimen in question. There are many cases of parallelism involving one or more characters in the various phylogenetic lines of oreodonts.

Remains of *Merycoidodon culbertsonii* and its subspecies have presented the most difficult morphologic problem in the study of the oreodonts. There is considerable individual variation (more than in other oreodont species) and overlapping of characters (including size), especially in examples of *M. culbertsonii* and *M. c. osborni.* The average examples of the former have a longer skull and a proportionately longer facial region than do the average of the latter. There are, however, examples of both the species and the subspecies that overlap and are not separable. The divisions become less obvious as more specimens become available.

The fact must also be considered that all these examples did not come from a single geological horizon of faunal "Zone A" of the Brule. The thicknesses of the deposits involved vary from 45 feet to more than 100 feet. Hence, a certain amount of variation is due to differences in geologic occurrence within "Zone A" of the Brule. The period of geologic time involved in the deposition of sediments representing this faunal zone was long enough to allow for a certain amount of development within a phylogenetic line.

The problem of identifying examples of *M.*

[1] Schultz and Falkenbach, 1956, p. 384.
[2] 1924, p. 127.
[3] 1940, p. 671.
[4] 1954, p. 224.
[5] 1937, p. 54.
[6] Schultz and Falkenbach, 1949, chart 3, p. 83.

culbertsonii and *M. c. osborni* is perhaps due to the fact that the two forms represent two phylogenetic lines that are close to the initial point of divergence and not far enough along in their separate lines of development to be easily distinguishable.

An outstanding example of individual variation may be observed in two associated skulls, F:A.M. 45217A and B, and in two additional associated individuals, F:A.M. 72246A and B. (See p. 58 for detailed discussion, and measurements, chart 4, fig. 1.)

The mounted skeleton (composite), A.M. 594 and 1287, has long been accepted as a typical example of *M. culbertsonii.* The present writers believe that the two individuals involved in the composite mount are actually examples of *M. culbertsonii* (A.M. 594, see p. 42) and *M. c. osborni* (A.M. 1287, see p. 59).

The F:A.M. collections from South Dakota and North Dakota were made by Morris F. Skinner and associates (Ralph Mefferd, 1939, 1940; Ralph Mefferd and Gordon Fletcher, 1938; Ove Kaisen and Morris F. Skinner, Jr., 1944; Ove Kaisen, Leonard Nelson, and Morris F. Skinner, Jr., 1945; Thomas Lucas and Morris F. Skinner, Jr., 1950; Robert E. Lamb, Morris F. Skinner, Jr., and Loren M. Toohey, 1951; Alan L. Lamb, Thomas Lucas, and Morris F. Skinner, Jr., 1953; and Morris F. Skinner, Jr., and Loren M. Toohey, 1954); and those from Wyoming by Charles H. Falkenbach and associates (John C. Blick, Everett De Groot, Gene Roll, and George Sternberg, 1938, 1939, 1943, 1944, 1945, 1948, 1953, 1954). The U.N.S.M. collection was made by E. L. Blue, T. M. Stout, C. Bertrand Schultz, and associates, 1933–1941.

One hundred and sixty-one specimens are here recorded:

COTYPES

Partial right maxilla with M^2–M^3 (erupt.). (–M)	A.N.S.P. 10728	From "Zone A" of Brule Formation, White River, South Dakota; collected by Thaddeus A. Culbertson Figured by Leidy, 1848, figs. 1–2; Thorpe, 1937, figs. 21a–21b
Partial right ramus with M_1–M_3 (erupt. br.). (–M)	10727	Figured by Leidy, 1852a, figs. 3–5; Thorpe, 1937, figs. 21c–21d This report, figure 3

The above cotypes have the same data and were both collected by Thaddeus A. Culbertson. The examples are not quite mature and suggest that they are one individual.

REFERRED FROM (A) GENERAL AREA, SOUTH DAKOTA; (B) SHANNON, (C) PENNINGTON, (D) WASHABAUGH, (E) JACKSON, AND (F) HARDING COUNTIES, SOUTH DAKOTA; (G) SIOUX, (H) DAWES, AND (I) SCOTTS BLUFF COUNTIES, NEBRASKA; (J) NIOBRARA AND (K) CONVERSE COUNTIES, WYOMING; (L) STARK COUNTY, NORTH DAKOTA; (M) COLORADO; AND (M′) LOGAN COUNTY, COLORADO

A. FROM SOUTH DAKOTA[1]

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–M^3 and mandible with I_1–M_3. (W)	U.S.N.M. 2506	Collected by John Evans (or Alexander and Thaddeus Culbertson), 1852 Figured by Leidy, 1854a, pl. 2, figs. 1–2

The above mandible has styles between the hypocone and protocone of the molars, well developed on M_3.[2]

MANDIBULAR RAMUS

		A.N.S.P.
Partial right ramus with P_2 (rt.)–M_3 . . . . Collected by Joseph Jeanes.	(W)	10726

[1] Exact localities uncertain.
[2] See Schultz and Falkenbach, 1940, p. 235, fig. 9.

FROM "OREODON BEDS," AMERICAN MUSEUM EXPEDITION, 1892:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS — A.N.S.P.

Skull with I^1–M^3, mandible with I_1–M_3 (I_3–P_1 br.), partial scapula, right humerus, distal ends of radius and ulna, metacarpals 2, 4, and 5, pelvis, 2 femora, tibia, fibula, cuboid, phalanges 2 and 4, calcaneum, all precaudal vertebrae, and caudals 1–3, and 5–12 . . . . (w) A.M. 594

The skull, mandible, scapula, cervical and dorsal vertebrae, and caudals 5–12 included in composite mount, A.M. 1287. Figured (in part) by Osborn, 1910, fig. 106; Scott, 1913, figs. 136, 204A; O'Harra, 1920, pl. 20, fig. B; Scott, 1940, fig. 133, p. 653.

It is here considered that the skull, mandible and skeletal elements of A.M. 594 are of an example of *M. culbertsonii*, and the skeletal elements of A.M. 1287 are *M. c. osborni* (see p. 59).

3 SKULLS AND MANDIBLES

Partial skull with I^1–M^3 (C/rt.) and partial mandible with I_1 (rt.) M_3(br.) (I_2–/C alv.). (M+)	A.M. 9793	From "Indian Creek Basin"; collected by Albert Thomson, 1902

American Museum catalogue states "middle *Oreodon*."

Partial skull with I^1–dP^2–M^2 (germ) (C/ erupt.) and mandible (attached) with I_1–dP_2–M_1 (P_1 erupt.). (I)	1305	From "Cheyenne River"; collected by A.M. exp., 1894
Skull and mandible	Y.P.M. 12754	From "middle Oligocene, upper nodular layer" (recorded by Thorpe, 1921f, p. 337)

2 SKULLS

Skull with I^1–M^3. (w)	Y.P.M. 12094	From "White River"; collected by J. Egan, 1875

Recorded by Thorpe, 1937, p. 54, "with well developed single-rooted accessory premolar between canine and normal first premolar on both sides."

Skull with I^1–I^2 alv. and I^3–M^3. (w)	A.M. 12319	From "Silas Ranch, Pass Creek, Cheyenne River"; collected by Albert Thomson, 1904

B. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 2 MI. W. OF SHEEP MT.:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 SKULLS AND MANDIBLES

		F.A.M.
Skull with I^1–M^3 and mandible (attached) with I_1–M_3	(M+)	45148
Partial skull with C/–P^1 rt. and P^2–M^3(br.) (M^2 br.) and partial mandible with P_3–M_3	(M+)	45153

3 SKULLS

Partial skull with I^1–C/ rt. and P^1–M^3 . . . . (w‡) 45065

The field data for above specimen state "Middle *Oreodon* beds" (="Zone B"). However, the small auditory bullae of the skull are equal to those of *M. culbertsonii* from "Zone A" of the Brule.

Partial skull with P^2–M^3	(w)	45146
Partial skull with I^1–I^3 rt. and C/–M^3 (P^1 rt.)	(w+)	45174

GROUP II (OBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Anterior portion of skull with I^1–I^3 rt. and C/(br.)–M^3 and mandible with I_1(rt.)–M_3 . . . . (M+) 45240

FROM 3 MI. W. OF SHEEP MT.:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

3 SKULLS AND MANDIBLES		F:A.M.
Partial skull with I^3(br.)–M^3 and partial mandible with P_1–M_3	(w+)	45231
Partial skull with I^1–P^1 br. and P^2–M^3 and mandible (attached) with I_1–/C br. and P_1–M_3	(w)	45237
Anterior portion of skull with I^1–M^3 (C/ br.) and partial mandible with I_1(rt.)–M_3 (P_1 rt.)	(w‡)	45247

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL		
Partial skull with I^1–C/ rt. and P^1–dP^2–M^3(erupt.)	(I)	72151

FROM WEST SIDE OF SHEEP MT.:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Partial skull with I^1(rt.)–M^3 and mandible (attached) with I_1–M_3	(w‡)	45140

FROM COTTONWOOD PASS[1]:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Partial skull with I^1–C/br. and P^1–M^3 and partial mandible with /C–P_4 br. and M_1–M_3	(w‡)	45137

FOLLOWING EIGHT COTTONWOOD PASS LOCALITIES IN DIVIDE AREA BETWEEN WHITE RIVER AND CHEYENNE RIVER DRAINAGES

FROM ½ MI. N. OF COTTONWOOD PASS:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 SKULLS AND MANDIBLES		F:A.M.
Skull with I^2–M^3 (I^3 br.) and mandible with I_1–M_3	(w)	45147
Skull with I^1–I^2 br. and I^3–M^3 and mandible with I_1–P_1 br. and P_2–M_3	(w)	72150

SKULL		
Skull with I^1–M^3	(w)	72153

The above dentition has a pronounced style at the base of each molar tooth between the hypocone and protocone.

FROM 1 MI. N. OF COTTONWOOD PASS:

GROUP II (OBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with I^1–I^3 br. and C/–M^3 and mandible with I_1–M_3	(w)	72154

FROM 1½ MI. N. OF COTTONWOOD PASS:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Anterior portion of skull with I^1–I^2 rt. and I^3–M^3 and partial mandible (attached) with I_1(rt.)–M_3	(w)	45141

[1] Cottonwood Pass actually is in the divide area between the Cheyenne River and White River drainages.

FROM N. SIDE OF COTTONWOOD PASS:

GROUP QUESTIONABLE (NASALS MISSING) F:A.M.

SKULL AND MANDIBLE

Partial skull with I^1–I^3 rt. and C/–M^3 (P^3 rt.) and partial mandible with P_1(rt.)–M_3 (br.) . . . . . (M) 72152

The field data state that the above specimen was from the "Middle *Oreodon* beds" (="Zone B"), but the specimen has small bullae which are equal to those of *M. culbertsonii* (see p. 33 for discussion).

FROM S. SIDE OF COTTONWOOD PASS:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Skull with I^1–I^2 br. and I^3–M^3 and mandible (attached) with I_1–I_2 rt. and I_3–M_3 . (W) 49679

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM 1½ MI. S. OF COTTONWOOD PASS:

SKULL

Partial skull with P^2(rt.)–M^3 . . . . . (M) 45034

FROM 1 MI. S. OF COTTONWOOD PASS:

GROUP II (OBTUSE POSTERIOR BORDER OF NASAL)

SKULL

Partial skull with I^1(rt.)–M^3 (C/ rt.) . . . . . (M) 45151

FROM BIG CORRAL DRAW AREA:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 SKULLS AND MANDIBULAR RAMI

Anterior portion of skull with I^1(alv.)–M^3 and right ramus with P^1–P^2 rt. and P^3–M^3 . (M+) 45234

Partial skull with I^1–M^3 (C/br.) and mandible (attached) with I_2–P_1 br. and P_2–M_3 . . . . . (W‡‡) 45249

The above skull has an exceptionally acute posterior border to the nasals.

SKULL

Partial skull with C/(rt.)–M^3 (P^1 alv.) . . . . . (W‡) 45254

FROM W. BIG CORRAL DRAW:

SKULL AND MANDIBLE

Partial skull with C/–dP^2–M^3(germ) and mandible (attached) with /C–dP_2–M_2 . (I) 72163

FROM E. FORK BIG CORRAL DRAW:

SKULL

Partial skull with I^1(rt.)–M^3 (C/ br.) . . . . . (W‡+) 45232

FROM AREA BETWEEN BIG AND LITTLE CORRAL DRAWS:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 ASSOCIATED SKULLS AND MANDIBLES (ATTACHED), IMMATURE

Skull with C/–dP^2–M^3(germ) and mandible with /C–dP_2–M_2, and metatarsal . . (I) 72162A

Skull with I^1–dP^2–M^2 (dP^3–dP^4 br.) and mandible with I_1–dP_2–M_2 (dP_3–dP_4 br.) . (I) 72162B

The above two specimens were found associated in the field.

FROM LITTLE CORRAL DRAW AREA:

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

2 SKULLS AND MANDIBLES (ATTACHED) F:A.M.

Skull with I^1–M^3 and mandible with I_1–I_2 and I_3–M_3 . . . . (M) 45227
Premolars larger than usual in this species.
Skull with C/(br.)–M^3 and mandible with I_1–I_3 br. and /C–M_3 . . . . (M) 45229

GROUP QUESTIONABLE (LACKING NASALS)

2 SKULLS

Partial skull with I^2(alv.)–M^3 (I^3–C/ rt., P^2–P^4 br.) . . . . (w‡‡) 45096
Anterior portion of skull with I^3–C/ rt. and P^1–M^3 . . . . (w‡‡) 45152

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM HEAD OF BATTLE CREEK DRAW:

SKULL AND MANDIBLE

Partial skull with I^1–M^3 and mandible with I_1–M_3 (P_1 br.) . . . . (w‡⁺) 45142

FROM BETWEEN BATTLE CREEK DRAW AND BATTLE CREEK CANYON:

SKULL AND MANDIBLE

Partial skull with I^1–C/br. and P^1–dP^2–M^3(erupt.) and mandible (attached) with I_1–I_3 br. and /C–dP_2–M_3(erupt.) . . . . (I) 72155

GROUP QUESTIONABLE (LACKING NASALS)

SKULL AND MANDIBLE

Anterior left side of skull and mandible with P_1(rt.)–M_3 . . . . (w) 72156

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

2 SKULLS

Partial skull with I^1(br.)–M^3 . . . . (w) 45057
Anterior portion of skull with I^1–C/ rt. and P^1–M^3 . . . . (w) 45144

GROUP QUESTIONABLE (POSTERIOR NASAL BORDER MISSING)

Partial skull with I^1–M^3 . . . . (w) 72165

B′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1 MI. E. OF COTTONWOOD PASS:

GROUP QUESTIONABLE (NASALS MISSING)

MAXILLAE AND MANDIBLE F:A.M.

Partial left and right maxillae with P^2–M^3 and partial mandible with P_2–M_3 . . . (w) 72170

C. FROM CHEYENNE RIVER DRAINAGE, WEST SIDE OF SADDLE HORSE PASS,[1] PENNINGTON COUNTY, SOUTH DAKOTA

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with I^1–M^3, mandible with I_1–M_3, partial tibia, partial fibula, partial pes, and vertebrae. Figures 1–3; Schultz and Falkenbach, 1956, fig. 4 (in part) . . . . . (w‡) F:A.M. 45155

[1] Saddle Horse Pass in the divide area between the Cheyenne River and White River drainage.

C′. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM 1–1½ MI. E. AND 4 MI. N. OF IMLAY:

3 SKULLS AND MANDIBLES — F:A.M.

Partial skull with P^2–M^3 and partial mandible with P_1(rt.)–M_3 . . . . (w) 45041

Anterior portion of skull with I^2(rt.)–dP^2–M^2 and partial mandible (attached) with I_1–P_1 br. and dP_2–M_2 . . . . (I) 72157

Partial skull with I^1–I^3 br. and C/(erupt.)–dP^2–M^2(erupt.) and partial mandible (attached) with I_1–/C br. and P_1 (erupt.)–dP_2–M_1 . . . . (I) 72158

MANDIBLE

Partial mandible with I_1–M_3 . . . . (w+) 72159

FROM 2½ MI. E. AND 4 MI. N. OF IMLAY:

SKULL

Partial skull with I^1–M^3 . . . . (w‡) 45037

FROM 1 MI. E. OF IMLAY:

SKULL

Partial skull with P^3(rt.)–M^3 (P^4 br.) . . . . (w+) 45115

FROM ½–¾ MI. S. OF IMLAY:

SKULL AND MANDIBLE

Anterior portion of skull with C/–M^3 and partial mandible (attached) with I_1–P_1 br. and P_2–M_3 . . . . (w‡) 45210

GROUP QUESTIONABLE (NASALS MISSING)

SKULL

Partial skull with I^1–C/ br. and P^1–M^3 (P^2 rt.) . . . . (M+) 45202

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM SCENIC AREA (COLLECTED BY ALBERT THOMSON):

SKULL — A.M.

Partial skull with I^3(rt.)–M^3 . . . . (M) 39413

FROM S. OF SCENIC (COLLECTED BY WALTER GRANGER, 1941):

SKULL

Partial skull with I^1–I^3 alv. and C/–M^3 . . . . (w‡) 39461

(COLLECTED BY ALBERT THOMSON, 1941):

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^1(br.)–M^3 (I^3 br.), mandible (attached) with I_1–M_3(I_3 br.), partial radius; partial ulna, 2 partial manus, partial tibia, astragalus, calcaneum, and partial pes . . . . (w) 48822

SKULL

Partial skull with I^1–M^3 . . . . (w‡$^+$) 48818

FROM CAIN CREEK, 2 MI. N. OF IMLAY:

GROUP QUESTIONABLE (NASALS UNDETERMINED)

3 ASSOCIATED SKELETONS		S.D.S.M.
Mounted skeleton	(M)	28129
Partial skeleton	(I)	
Partial skeleton	(I)	

The above three individuals were found associated in one field block. The two (I) immature are actually fetal and were found within the pelvic girdle of the (M) mature individual.

Thorpe[1] referred an immature skull and mandible, S.D.S.M. "311" (=31133) to this species, and considered the specimen one of the fetal twins, S.D.S.M. 28129. (See discussion, p. 382.)

Scott[2] also referred the same skull and mandible to this species, but did not associate it with the fetal twins. (See discussion, p. 382.)

Actually, the adolescent specimen, S.D.S.M. 31133, is from Colorado and is referable to the Miniochoerinae. (See p. 434.)

FROM MILLER BASIN, CAIN CREEK AREA:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 SKULLS AND MANDIBLES		F:A.M.
Anterior portion of skull with C/–P^1 br. and P^2–M^3, and mandible with M_1–M_3	(W)	45039
Partial skull with C/(rt.)–M^3 and partial mandible with P_4–M_3	(M)	45160
SKULL AND LIMB ELEMENTS		
Skull with I^1–M^3, partial femur, and partial tibia	(M+)	45200
4 SKULLS		
Partial skull with C/–P^2 rt. and P^3–M^3	(W)	45136
Partial skull with I^2(rt.)–M^3	(W)	45163
Partial skull with I^2–C/ br. and P^1–M^3	(W‡)	45203
Partial skull with C/–P^1 br. and P^2–M^3	(M+)	72166

GROUP II (OBTUSE POSTERIOR BORDER OF NASALS)

3 SKULLS		
Partial skull with I^3(alv.)–M^3 (C/ rt.)	(M+)	45219
Skull with I^1–M^3 (C/ br.)	(W+)	72167
Partial skull with dP^1–M^3(germ)	(I)	72168

GROUP QUESTIONABLE (POSTERIOR NASAL BORDER MISSING)

3 SKULLS AND MANDIBLES (ATTACHED)		
Partial skull with C/(br.)–M^3 and mandible with I_1–P_1 br. and P_2–M_3	(M)	45197
Partial skull with P^2–M^3 and mandible with P_1(br.)–M_3	(W+)	45212
Partial skull with P^2(br.)–dP^3–M^2 and mandible with I_1–/C alv. and P_1–dP_2–M_2	(I)	72169
MANDIBLE		
Partial mandible with I_1–P_1 rt. and P_2–M_3	(W)	72171

FROM E. SIDE OF SADDLE HORSE PASS:

GROUP QUESTIONABLE (NASALS MISSING)

SKULL AND MANDIBLE (IMMATURE)		
Partial skull with C/(br.)–dP^2–M^3(germ) and partial mandible (attached) with /C–dP_2–M_2	(I)	72160

[1] 1937, p. 55, pl. 2, figs. 3–4.
[2] 1940, p. 656, pl. 70, fig. 1.

FROM 4 MI. SE. OF SCENIC:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

		F:A.M.
Skull with I^1–I^2 alv. and I^3–M^3, mandible with I_1–M_3, 2 femora, 2 tibiae, 2 astragali, 2 calcanea, 2 partial pedes, pelvis, and vertebrae. Figures 21–23, 51 (in part)	(w)	45159
Skull with I^3(br.)–dP^2–M^3(germ), mandible (attached) with /C–P_1 br. and dP_2–M_2, 2 partial femora, 2 tibiae (1 partial), 2 astragali (1 partial), 2 calcanea, 2 partial pedes, pelvis, and vertebrae	(I)	72161

SKULL

Partial skull with I^1–M^3	(w+)	45114

The nasals of the above skull are unusually wide.

FROM CONATA AREA:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Partial skull with C/(br.)–M^3(P^4 br.) and partial mandible with P_1–P_2 rt. and P_3–M_3	(w‡)	45158

GROUP QUESTIONABLE (LACKING NASALS)

2 SKULLS

Anterior portion of skull with dP^3(br.)–M^3(germ)	(I)	72174
Anterior portion of skull with C/(rt.)–dP^2–M^3(erupt.) (P^1 br.)	(I)	72217

D. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM 2 MI. ABOVE MOUTH OF POTATO CREEK:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

		F:A.M.
Partial skull with I^2–P^1 br. and P^2–M^3 and partial mandible with P_1–P_4 br. and M_1–M_3	(w+)	45110

E. FROM WHITE RIVER DRAINAGE, HODGE'S BASIN, 9 MILES EAST OF INTERIOR, JACKSON COUNTY, SOUTH DAKOTA

MANDIBLE

		F:A.M.
Partial mandible with I_1–/C rt. and P_1–dP_3–M_3(erupt.)	(I)	72173

F. FROM SLIM BUTTES AREA, HARDING COUNTY, SOUTH DAKOTA

FROM 1 MI. N. OF SLIM BUTTES BATTLE MONUMENT:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Skull with I^2–M^3 (I^3 br.) and mandible (attached) with I_1–M_3	(M)	72175

FROM REVA GAP:

MAXILLA AND MANDIBULAR RAMUS

Partial left maxilla with P^4(br.)–M^2(br.) and partial left ramus with M_1–M_3	(w‡+)	72178

FROM 2 MI. SOUTH OF REVA GAP:

MANDIBLE

Partial mandible with I_1(br.)–M_3(br.) (/C–P_1 br.)	(w)	72179

FROM HEAD OF POINT CREEK:

2 MANDIBULAR RAMI		F:A.M.
Partial mandible with I_1–I_3 rt. and /C–M_3 (P_1 br.)	(W)	72176
Partial left ramus with P_1–P_3 rt. and P_4(br.)–M_3(br.)	(M)	72177

G. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM MENG RANCH AREA (U.N.S.M. COLL. LOC. SX–12 TO 14):

GROUP II (OBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		F:A.M.
Partial skull with I^2–M^3 (I^3, P^1, and M^1–M^3 br.) and partial mandible with I_2–I_3 br. and /C–M_3(br.)	(W)	72311

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL		
Partial skull with I^1–P^2 rt. and P^3–M^3	(W‡)	72241

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL, MANDIBLE, AND VERTEBRAE		
Crushed partial skull with I^1–I^2 alv. and I^3–M^3, partial mandible (attached) with I_1–M_3, and vertebrae	(W)	72202
SKULL AND HUMERUS		
Partial skull with P^4–M^3 and partial humerus	(W‡+)	72204
3 SKULLS		
Partial skull with C/–M^3	(W‡+)	72203
Partial skull with C/–P^2 rt. and P^3–M^3	(W)	72205
Partial skull with C/(rt.)–M^3	(W‡)	72242

FROM E. END OF HAT CREEK BASIN, N. OF HARRISON (U.N.S.M. COLL. LOC. SX–7):

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Partial skull with I^1–M^3 and mandible (attached) with I_1–I_3 rt. and /C(br.)–M_3	(M)	72206

FROM U.N.S.M. COLL. LOC. SX–4:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Skull with I^2–M^3 and mandible with I_1–M_3	(M)	28095

Incisors and premolars more like those of *Paramerycoidodon georgei.*

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with I^1–M^3 and mandible with I_1–M_3	(W‡)	28086

FROM U.N.S.M. COLL. LOC. SX–8:

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Partial skull with I^1–I^2 alv. and I^3–M^3 and mandible with I_1(rt.)–M_3 (P_1 br.)	(W+)	28331

FROM WARBONNET RANCH, NORTH OF HARRISON:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

			Y.P.M.
Partial skull with P^2(br.)–M^3, partial mandible with P_3–M_3, partial tibia, and partial pes . . . . Collected by F. W. Darby, 1914.	(W+)		12238

MOUNTED SKELETON

Most of skeleton 12239
Collected by W. S. Benton, 1914. Figured by Thorpe, 1923a, fig. 1 (in part); 1923b, figs. 5–6.

G′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM U.N.S.M. COLL. LOC. SX–17:

SKULL AND MANDIBLE — U.N.S.M.

Partial skull with I^1–M^3 and partial mandible with I_1–I_2 rt. and I_3–M_3 . . . . . (W‡) 28090

FROM U.N.S.M. COLL. LOC. SX–18:

SKULL AND MANDIBLE

Partial skull with I^1(alv.)–M^3 and mandible with I_1–M_3 . . . . (M+) 28076

GROUP QUESTIONABLE (NASALS MISSING)

SKULL

Partial skull with P^1–M^3 . . . . (W‡) 28144

FROM U.N.S.M. COLL. LOC. SX–23:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Partial skull with I^1–I^3 rt. and C/–M^3 and mandible with I_1–M_3 (I_2 rt.) . . . . . (M) 28091

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

FROM U.N.S.M. COLL. LOC. SX–24:

SKULL

Partial skull with C/(rt.)–M^3(br.) (P^1–P^3 br.) . . . . (M+) 28617

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

FROM U.N.S.M. COLL. LOC. SX–25:

SKULL

Partial skull with C/(rt.)–M^3 (P^1 br.) . . . . (M+) 28078

FROM U.N.S.M. COLL. LOC. SX–26:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–I^2 alv. and I^3–M^3 and mandible with I_2–M_3 . . . . (W‡) 28062

GROUP II (OBTUSE POSTERIOR BORDER OF NASALS)

SKULL

Partial skull with P^2–M^3 . . . . (M+) 28071

FROM U.N.S.M. COLL. LOC. SX–27:

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Partial skull with I^1–M^3 and mandible with I_1–M_3.	(w)	28102

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM U.N.S.M. COLL. LOC. SX–29:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with I^1–M^3, mandible with I_1–I_2 rt. and I_3–M_3 (P_1 br.), partial femur, partial pelvis, and vertebrae	(w+)	28329

FROM U.N.S.M. COLL. LOC. SX–30:

SKULL		
Partial skull with C/–M^3 (P^1 and P^3 br.)	(w‡)	28092

FROM U.N.S.M. COLL. LOC. SX–31:

SKULL AND MANDIBLE		
Partial skull with P^1–M^3 and mandible with P_1(rt.)–M_3	(w+)	28068

FROM U.N.S.M. COLL. LOC. SX–32:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Partial skull with I^1–I^2 rt. and I^3–M^3, partial mandible with I_1–/C rt. and P_1–M_2(br.), radius, ulna, partial manus, partial femur, tibia, calcaneum, and partial pes. Figure 23 (in part)	(w‡+)	28467
SKULL		
Partial skull with P^2 (rt.)–M^3	(w‡)	28181

The last lobe of the above M^3 is greatly reduced laterally.

FROM SIOUX COUNTY,[1] NEBRASKA:

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE		
Partial skull with I^1 (br.)–M^3 and mandible with I_1–M_3	(w‡+)	28330

FROM WHITE RIVER REGION,[1] NEBRASKA:

SKULL		Y.P.M.
Partial skull (lacking bulla evidence)		12101

H. FROM WHITE RIVER DRAINAGE, DAWES COUNTY, NEBRASKA

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

FROM U.N.S.M. COLL. LOC. DW–104:

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Partial skull with I^1–M^3 and mandible with I_1–M_3.	(w)	28103

FROM WALTER BRECHT RANCH (= U.N.S.M. COLL. LOC. DW–104):

SKULL		F:A.M.
Crushed skull with I^1–M^3	(w‡)	72208

[1] Exact locality not known to present writers.

FROM U.N.S.M. COLL. LOC. DW–105:

GROUP QUESTIONABLE (NASALS MISSING)

SKULL		U.N.S.M.
Partial skull with C/(br.)–M^3(br.) (P^1 br.)	(M)	28037

I. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF MONUMENT, SCOTTS BLUFF COUNTY, NEBRASKA

		Y.P.M.
Partial mandible		12477

Specific identification questionable. (Referred "*Merycoidodon culbertsonii,*" by Thorpe, 1921f, p. 334.)

J. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SHACK DRAW AREA:

2 ASSOCIATED INDIVIDUALS

		F:A.M.
Mandible with I_1–M_3, humerus, 2 radii (1 partial), 2 ulnae, partial femur, tibia, astragalus, calcaneum, metapodial, partial pelvis, and vertebrae. Figures 19, 20 (in part)	(W)	72186A

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

Partial skull with I^2(br.)–M^1(erupt.) (P^1–dP^2 br.), partial mandible, I_1–P_1 rt. and dP_2–M_1, partial ulna, and 2 partial femora	(I)	72186B

The above individuals were found associated in the field.

2 SKULLS

Skull with I^1–I^2 rt. and I^3–M^3 (C/ br.)	(M+)	45063
Skull with C/(br.)–M^3 (P^1 br.)	(W‡+)	72189

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBULAR RAMUS, IMMATURE

Partial skull with C/(br.)–dP^1–M^2 and right ramus with I_2–dP_2–M_3(germ)	(I)	72187

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

2 SKULLS AND MANDIBLES

Anterior right side of skull with P^1–M^3(br.) and partial mandible with P_3–M_3	(M+)	45130
Skull with I^1(br.)–M^3 and mandible (attached) with I_1–M_3	(W)	72190

SKULL

Partial skull with I^1–C/ rt. and P^1–M^3(br.)	(M)	72191

FROM SPRING DRAW AREA:

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND SKELETAL ELEMENTS

Partial skull with C/–P^1 rt. and P^2(br.)–M^3 (P^3–P^4 br.), partial humerus, femur, partial tibia, astragalus, 2 calcanea, and vertebrae	(W‡+)	45133

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

4 SKULLS AND MANDIBULAR RAMI

Skull with I^1–P^2 rt. and P^3–M^3 and mandible (attached) with I_1–P_2 br. and P_3–M_3	(M)	45123
Partial skull with I^1–M^3 and right ramus with I_1(rt.)–M_3 (I_2, P_1 br.)	(W)	45127

Above premolars approaching size of examples of *Paramerycoidodon georgei.*

		F:A.M.
Right side of skull with I^1–M^3 (C/ br.) and partial left ramus with P_4–M_3(br.) . .	(w‡+)	45129
Anterior portion of skull with I^1–M^3 (C/ br.) and partial right ramus with M_3 . .	(M+)	45131

SKULL

Partial skull with C/(rt.)–M^3 . . . . (w‡) 45132

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–M^3 (P^1 br.) and mandible with I_1–M_3 . . . . (w‡) 45125

SKULL

Skull with I^1–M^3 . . . . (M+) 72192

FROM WHITMAN POST OFFICE AREA, DUE NORTH OF NODE:

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Skull with I^1–dP^2–M^3(germ), mandible (attached) with I_1–dP_2–M_2, humerus, radius, ulna, partial manus, pelvis, and vertebrae . . . . (I) 72193

Skull with I^1–M^3, mandible with I_1–M_3, partial pelvis, and fragments . . . . . . (M+) 72194

2 SKULLS AND MANDIBULAR RAMI

Partial skull with C/–dP^2–M^2(erupt.) and mandible (attached) with I_1–dP_2–M_2 . (I) 72195

Partial skull with C/–P^2 br. and P^3–M^3 and partial left ramus with M_1(rt.)–M_3(br.) . . . . (W) 72196

FROM N. INDIAN CREEK ROAD AREA, S. AND E. OF SEAMEN[1] HILLS:

GROUP QUESTIONABLE (POSTERIOR BORDERS OF NASAL MISSING)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Crushed skull with C/–M^3, mandible with /C–P_2 br. and P_3–M_3, and partial pelvis . . . . (M) 72197

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL

Partial skull with P^1(br.)–M^3 . . . . (W) 45107

GROUP II (SUBOBTUSE POSTERIOR BORDER OF NASALS)

SKULL

Skull with I^1–C/ rt. and P^1–M^3 . . . . (W) 45105

FROM MILL'S FALLS, W. OF U. S. HIGHWAY NO. 85:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL

Partial skull with C/–M^3. . . . . (w‡) 45083

FROM SEAMEN HILLS AREA:

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE

Partial skull with I^2–I^3 rt. and C/(br.)–M^3 and mandible with I_1(rt.)–M_3 . . . . (M+) 72198

SKULL

Partial skull with I^1–M^3 (C/br.) . . . . (W+) 72199

[1] It is our understanding that Seamen was a family name and originally spelled "Seamen"; however, it occasionally appears as Seemen.

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		F:A.M.
Partial skull with I^1–M^3 (I^2 alv. and M^1–M^3 br.), partial mandible with I_1–M_3 (/C br.), partial pelvis, and vertebrae	(w+)	72310

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1(rt.)–M^3 and mandible with I_1–M_3	(w)	72200

K. FROM 8 MILES SOUTHEAST OF DOUGLAS, CONVERSE COUNTY, WYOMING

GROUP QUESTIONABLE (NASALS MISSING)

SKULL AND MANDIBLE		F:A.M.
Fragments of skull with C/(rt.)–M^3 (P^4 br.) and partial mandible with I_1–M_3(br.) (P_1–P_2 br.)	(w‡+)	72201

L. FROM LOWER PART OF THE NODULAR ZONE, SOUTH OF SOUTHHEART, STARK COUNTY, NORTH DAKOTA

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		F:A.M.
Partial skull with I^1–M^3 (P^1 br.), partial mandible with I_1(rt.)–M_3 (/C–P_1 rt.) 2 partial tibiae, 2 astragali, 2 partial calcanea, partial pes, vertebrae, and fragments	(M+)	72180

2 SKULLS AND MANDIBULAR RAMI

Partial skull with P^1–M^3(br.) and mandible with I_1–I_2 rt. and I_3–M_3	(w+)	72181
Anterior portion of skull with I^1–I^3 rt. and C/(br.)–M^3, partial left ramus with M_2(br.)–M_3, and partial calcaneum	(w‡+)	72182

SKULL

Partial skull with I^2–C/ rt. and P^1–M^3	(M+)	72183

GROUP QUESTIONABLE (POSTERIOR BORDER OF NASALS MISSING)

SKULL AND FRAGMENTS

Partial skull with I^1–I^2 rt. and I^3–M^3 and ramal fragments	(M+)	72184

SKULL

Anterior portion of skull with C/–M^3 (P^1 br.)	(w+)	72185

M. FROM GERRY'S RANCH, COLORADO

SKULL		Y.P.M.
Partial skull		12586

Collected by Henry B. Sargent, Yale College Scientific Expedition of 1872.

GROUP I (ACUTE POSTERIOR BORDER OF NASALS)

SKULL AND MANDIBLE (ATTACHED)		A.M.
Partial skull with C/–M^3 and mandible with I_1–M_3	(w)	8907

Collected by H. T. Martin, 1898.

From oreodont faunal "Zone B" of the Brule Formation; tentatively referred remains from Washabaugh County, South Dakota

One specimen is here recorded:

FROM W. SIDE OF PASTURE CREEK, SW. OF CONATA:

GROUP QUESTIONABLE (LACKING POSTERIOR BORDER OF NASALS)

SKULL AND RADIUS		F:A.M.
Partial skull with C/(rt.)–M^3 and partial radius	(M)	45113

2a. **Merycoidodon culbertsonii browni,**[1]
new subspecies

From "Zone C" of the Chadron Formation, Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; Dawes and Sioux counties, Nebraska; Shannon County, South Dakota

DESCRIPTION

SKULL: Within size range of *M. culbertsonii;* narrower and lighter than average examples of the species. (See generic characters.)

MANDIBLE: Size comparison same as for skull; post-symphysis below P_3; inferior border of ascending ramus with less inward curve than examples of *M. culbertsonii.* (See generic characters.)

DENTITION: Same size comparison as skull; series more massive than average examples of the species; P^1–P^3 each with moderately prominent anterior intermediate crest. (See generic characters.)

LIMBS: Tendency to be lighter than examples of *M. culbertsonii.* (See generic characters.)

MEASUREMENTS: Tables 1 and 7 (pp. 35 and 146).

ILLUSTRATIONS: Figures 1–3, 19–23.

DISCUSSION

Remains of the new subspecies, *Merycoidodon culbertsonii browni,* are not well represented in the collections. The holotype, however, is an almost complete skeleton. It is of interest that Charles F. Falkenbach (son of one of the authors) found the skull and mandible of a saber-tooth cat exposed, and in the collecting found the complete cat skeleton. In preparing the tail vertebrae of the cat, we found a second string of caudals on top of the first, and in due time the second tail was found to be a part of another skeleton. In the field, it was taken for granted (without completely uncovering the remains) that here was a second cat (perhaps immature). In the laboratory, however, the second individual was found to be an almost complete adult oreodont skeleton, the holotype of the new subspecies.

The oreodont had not been damaged by the cat. Perhaps the cat had killed the oreodont, but, not being hungry, turned its back on its prey and had fallen asleep. The cat apparently died suddenly, and the two animals remained in their natural positions until the discovery in 1953.

The size range of the few examples of *M. c. browni* from "Zone C" of the Chadron is within the range found in those of the species from "Zone A" of the Brule. There is considerable variation in the width and length of the dentition. The teeth of the holotype are wider and more massive than even the average examples of *M. culbertsonii* from the Brule deposits above. It is here suggested that examples like the holotype, which has a lighter dentition, gave rise to *M. culbertsonii,* and that those with the heavier teeth represent a separate branch.

In the present revision of the oreodonts, the stratigraphic occurrences of the fossils have been stressed. The various phylogenetic lines have been established with the aid of the geologic data associated with the specimens. Usually, when there is an obvious break in the morphological development within a phylogenetic line, the break coincides with some type of geologic phenomenon. Where there is a major hiatus between two terrestrial deposits, there is invariably evidence of an unconformity or the presence of a paleosol complex. The geological processes that caused the breaks appear to have been more than regional and influenced most of western North America, since the faunal breaks are widespread geographically. This conclusion, of course, is based on the geographic and geologic distribution of the oreodonts as well as on the stratigraphic correlations of the deposits involved. The major oreodont faunal changes and breaks are shown very strikingly on charts 15 and 16. Unfortunately, an abundance of examples of oreodonts has not been found in deposits of Chadron age.

There is no apparent faunal break between the Chadron and the Brule, but there is a major one between the sediments of faunal zones "A" and "B" of the Brule. The latter faunal break represents a considerable period of geological time, perhaps as much as or even more than can be attributed to the deposition of sediments of faunal zones "B," "C," and "D" of the Brule (see faunal break indicated on chart 16). This is demonstrated in part by the comparison of skulls of *Merycoidodon culbertsonii* from "Zone A" of the Brule and those of *M. c.*

[1] Named in honor of the late Dr. Barnum Brown of the American Museum of Natural History.

browni from "Zone C" of the Chadron. The skulls of these two forms have very similar characters, although examples of *M.* (*Anomerycoidodon*) *dani* ("Zone B" of the Brule) are very distinct from those of *M. culbertsonii* (from "Zone A") and much more like those of *M.* (*A.*) *lambi* ("Zone D" of the Brule).

The F:A.M. specimens from Wyoming were collected by Charles H. Falkenbach and associates (1944, 1953); the F:A.M. examples from Nebraska, by Morris Skinner and associates, 1953; and the U.N.S.M. material from Nebraska, by C. Bertrand Schultz and associates, 1938, and Cyril Harvey, Lloyd Tanner, C. Bertrand Schultz, and associates, 1954.

Fifteen specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, 2 scapulae, 2 humeri, 2 radii, 2 ulnae, manus, 2 femora, 2 tibiae, fibula, 2 astragali, 2 calcanea, 2 pedes, ribs, vertebrae, and pelvis. (w)	F:A.M. 72286	From oreodont faunal "Zone C" of Chadron Formation, NW. end of Seamen Hills, channel 37′ below "Purplish White Layer," Cheyenne River Drainage, Hat Creek Basin, Niobrara County, Wyoming; collected by Alan L. Lamb, Charles F. Falkenbach, Charles H. Falkenbach, Morris F. Skinner, and Morris F. Skinner, Jr., 1953 Figures 1–3, 19–23

The manus of the holotype has five digits and the pes four.

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; (B) SIOUX AND (C) DAWES COUNTIES, NEBRASKA; AND (D) SHANNON COUNTY, SOUTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SE. END OF SEAMEN HILLS:

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with C/(br.)–dP^2–M^2, partial mandible with P_2–dP_3–M_3 (germ, br.), and partial pes	(I)	49764
Skull with I^2(rt.)–M^3, mandible with I_2–I_3 br. and /C–M_3, partial scapula, and partial humerus	(M+)	72287

3 SKULLS

Anterior portion of skull with C/(br.)–dP^2–M^3 (germ)	(I)	49765
Skull with C/–M^3 (P^2–P^4 erupt.)	(−M)	72288
Partial skull with I^1–M^3	(w‡⁺)	72289

B. FROM WHITE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM "BALD BUTTE":

MAXILLA

		F:A.M.
Partial left maxilla with M^1–M^2	(w‡)	49722

FROM U.N.S.M. COLL. LOC. SX–26:

SKULL AND MANDIBLE (ATTACHED)

		U.N.S.M.
Partial skull with I^1(alv.)–M^3 (M^1 absent) and mandible with I_1–M_3	(w‡‡)	28620A

The above specimen was collected from the "Upper Purplish White Layer," which is included in "Zone C" of the Chadron. The skull is wider than the holotype of *M. c. browni* and may represent a male example.

MAXILLA, IMMATURE

Partial right maxilla with P^2(br.)–dP^3–M^2	(I)	28620B

The above specimen was found associated with the preceding skull and mandible (U.N.S.M. 28620A).

Partial skull with I^3–M^3 and mandible with I_1–M_3 (P_1 br.)	(w)	28621

FROM 7 MI. N. AND 6 MI. W. OF CRAWFORD:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^1–M^3, partial mandible with I_1–M_3, partial ulna, partial radius, femur, partial tibia, astragalus, calcaneum, fragments of pes, partial pelvis, vertebrae, and ribs . . . . (w‡) U.N.S.M. 28618

C. FROM WHITE RIVER DRAINAGE, DAWES COUNTY, NEBRASKA

FROM WALTER BRECHT RANCH (=U.N.S.M. COLL. LOC. DW–104):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P^4(rt.)–M^3, partial mandible with M_1–M_3, partial scapula, 2 partial humeri, partial radius, partial ulna, partial femur, partial tibia, fragmentary vertebrae, and ribs . . . . (w‡+) F:A.M. 72290

The above dentition is lighter than usual in this subspecies and approaches dentitions of *M. culbertsonii.*

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^2–M^3 (P^1 br.) and partial mandible with P_1(rt.)–M_3 . . . . . (w‡+) 72291

MANDIBULAR RAMUS

Fragmentary right ramus with M_3 . . . . (M) 72292

D. FROM SHANNON COUNTY, SOUTH DAKOTA (COLLECTED BY WANLESS, 1922)

Skull with I^1–M^3 (C/ br. and P^1 rt.) . . . . (w+) P.U. 12764

Figured by Scott, 1940, pl. 69, fig. 1; pl. 70, fig. 2.

Sinclair (1924, p. 99), in referring to the above specimen, stated: "One specimen, with auditory bullae of rugged type, which I am unable to separate from *Oreodon culbertsoni culbertsoni*, was found by us in the uppermost part of the *Titanotherium* beds about 18 inches below the contact plane." The present writers consider the bulla and the size of the skull within the individual variation of examples of *M. c. browni.* Both Sinclair and Scott considered the specimen referable to *M. culbertsonii.*

2b. **Merycoidodon culbertsonii osborni,**[1] new subspecies

From oreodont faunal "Zone A"[2] of the Brule Formation, Shannon County, South Dakota; referred remains from general area, South Dakota; Shannon, Pennington, Jackson, and Harding counties, South Dakota; Sioux, Dawes, and Scotts Bluff counties, Nebraska; Niobrara and Converse counties, Wyoming; Stark County, North Dakota; Logan County, Colorado; and 2c, geologic variety, from "Zone C" of Chadron Formation, Sioux and Dawes counties, Nebraska; and Niobrara County, Wyoming

DESCRIPTION

SKULL: Within size range of examples of *Merycoidodon culbertsonii,* average smaller than mentioned examples; tendency to have shorter face (anteroposteriorly), and proportionately wider skull than those of *M. culbertsonii;* nasals with obtuse or acute posterior border.

MANDIBLE: Within size range of examples of *M. culbertsonii,* but tendency for less over-all length and more robustness.

DENTITION: Tendency for series to be less in over-all length than examples of *M. culbertsonii;* P^1–P^3 each with weak anterior intermediate crest.

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[1] Named in honor of the late Prof. Henry Fairfield Osborn of the American Museum of Natural History. Both of the present writers are indebted to Professor Osborn for his encouragement of their preliminary stratigraphic paleontologic research during the early 1930's.

[2] Two of the 254 specimens referred to this subspecies, F:A.M. Nos. 49672 and 72302, are from "Zone B."

CHART 4

Merycoidodon culbertsonii osborni, New Subspecies. Comparative Measurements[a] of Two Associated Skulls

	F:A.M. 45217A Left	F:A.M. 45217A Right	F:A.M. 45217B Left	F:A.M. 45217B Right	Per Cent of Difference[b]
Basal length	(177.5)	(177.5)	178.6	178.6	0.6
Width	117.6	117.6	105	105	10+
Width of brain case	59	59	52.5	52.5	13−
Postorbital constriction	(30.5)	(30.5)	27.5	27.5	10−
Interorbital width	(58)	(58)	50	50	14−
Distance between interorbital foramina	18.5	18.5	7	7	62+
Posterior border of nasals	Obtuse	Obtuse	Acute	Acute	—
Breadth of condyle	34	34	33	33	3−
Vertical height of orbit	(31.3)	31.3	28	29	10+
Depth of malar below orbit	—	16.8	17.7	—	5+
Distance from C to anterior border of orbit	(76.3)	—	75	75.5	2−
Distance from anterior border of orbit to supraoccipital wings	(136.5)	(136.2)	125.5	(126)	8+
Anteroposterior length of postglenoid process	8.3	8.7	8.3	8.5	5−
Transverse width of postglenoid process	18	21	17	18.5	19
C/–M^3, greatest anteroposterior length	99.5	(99)	96.5	97.2	3+
P^1–M^3, greatest anteroposterior length	(87.8)	(86.5)	84.5	86.1	4−
P^1–P^4, greatest anteroposterior length	(44.5)	44.5	(41)	43.2	8−
M^1–M^3, greatest anteroposterior length	47.5	47	43.4	(44.5)	9+
P^1, greatest anteroposterior length	—	—	10.3	10	3−
P^1, greatest width	—	—	7	6.4	20
P^2, greatest anteroposterior length	12.1	(11.7)	11.2	10.8	11−
P^2, greatest width	8.7	—	8.2	8.3	6−
P^3, greatest anteroposterior length	12.2	12.2	10.7	10.5	14−
P^3, greatest width	10	10.3	11.3	11.1	11+
P^4, greatest anteroposterior length	10.5	10.6	10	10.1	6−
P^4, greatest width	13.5	13.6	13.9	13.7	3−
M^1, greatest anteroposterior length	14.2	14.2	(14)	—	1+
M^1, greatest width	16.3	15.6	16	15.7	4+
M^2, greatest anteroposterior length	17.6	17.4	17	17	3+
M^2, greatest width	18.7	18.7	18.3	18.3	2+
M^3, greatest anteroposterior length	19.2	18.8	18	17.7	8−
M^3, greatest width	18.7	18.7	19	19	2−

[a] ( ), Approximate. All measurements in millimeters.
[b] Degree of variation based on the larger measurement.

Limbs: Within size range of examples of *Merycoidodon culbertsonii.*

Measurements. Tables 1 and 7 (pp. 35 and 146).

Illustrations: Figures 1–3, 19–23.

Discussion

The material here referred to the new subspecies *Merycoidodon culbertsonii osborni* is not always readily separated from examples of *M. culbertsonii,* and the division is based on apparent tendencies only. The smallest example of *M. c. osborni* can be distinguished from the largest example of *M. culbertsonii* on the size difference, *M. c. osborni* being smaller, having a shorter facial region, and being broader. When all the examples, however, are considered, it seems impossible to suggest more than subspecific differences.

In many respects, skulls of *M. c. osborni* resemble exaggerated examples of *Otionohyus wardi* which also occur in "Zone A" of the Brule. It is reasonable to suspect that during late Chadron and early Brule times there was a divergence of the various lines of the subfamily, but not far enough removed for examples of *M. culbertsonii* to be recognized as separable from those of *M. c. osborni.* Perhaps the latter actually represents a separate phylum. The ancestry for all the phyla of the Merycoidodontidae is discussed on page 398.

The teeth of this subspecies, like those of most Oligocene oreodonts, are not of diagnostic value as they are not separable from those of *M. culbertsonii* or those of the type of *M. macrorhinus.*

The geologic variant, from "Zone C" of the Chadron of Sioux County, Nebraska, is not diagnostically different from examples of *M. c. osborni* from "Zone A" of the Brule. This tends to strengthen the possibility that these two forms (*M. c. osborni* and the geologic variety) may represent two distinct phyla close to the point of divergence.

Skull examples F:A.M. 45217A and 45217B were found associated in the field. Chart 4 (p. 58) gives the comparative measurements of the two skulls. In some instances measurements of both sides of the same skull are listed in order to show variation within a single individual.

The comparative measurements of associated specimens shown in charts 4 and 5 (the latter based on 11 associated individuals) represent actual individual variation, that is, no geologic or geographic variation is involved. These 11 associated individuals, however, must be considered as members of a local population, or possibly a single family, and therefore do not represent the total individual variation to be expected in the population of a subspecies as a whole.

The major differences between the two associated skulls (chart 4) are: in F:A.M. 45217A, the posterior border of the nasals is obtuse and the distance between the supraorbital foramina is 18.5 mm.; in F:A.M. 45217B, the posterior border of the nasals is acute and the distance between the supraorbital foramina is 7 mm. (see fig. 1). Chart 5 (p. 120) cites the measurements of the dentitions of the 11 individuals of *O.* (*Otarohyus*) *bullatus.*

In a total of 114 skulls that had the posterior border of the nasals present, 32 of the posterior borders are obtuse and 82 are acute. The ratio is approximately equal to that found in the nasals of *M. culbertsonii.*

The F:A.M. specimens from South Dakota, North Dakota, and Nebraska were collected by Morris F. Skinner and associates, 1938–1940, 1944, 1951, 1952, 1954; those from Wyoming, by Charles H. Falkenbach and associates, 1938, 1939, 1943–1945, 1948, 1951, 1952, 1954; and the U.N.S.M. examples from Nebraska, by E. L. Blue, Mylan Stout, Marian and Bertrand Schultz, and associates, 1933–1942.

Two hundred and fifty-four specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, scapula, 2 humeri, 2 radii (1 partial), ulna, partial manus, 2 femora, 2 tibiae, fibula, astragalus, calcaneum, partial pes, pelvis, vertebrae, and ribs. (w+)	F:A.M. 49668	From "Zone A" of Brule Formation, "middle of lower nodules," 1½ mi. S. of Rock Springs in Big Corral Draw, Cheyenne River drainage, Shannon County, South Dakota; collected by Morris Skinner and party, 1940 Figures 1–3, 19–23

REFERRED FROM (A) SOUTH DAKOTA, (B) SHANNON, (C) PENNINGTON, (D) JACKSON, AND (E) HARDING COUNTIES, SOUTH DAKOTA; (F) SIOUX, (G) DAWES, AND (H) SCOTTS BLUFF COUNTIES, NEBRASKA; (I) NIOBRARA AND (J) CONVERSE COUNTIES, WYOMING; (K) STARK COUNTY, NORTH DAKOTA; AND (L) LOGAN COUNTY, COLORADO

A. FROM GENERAL AREA,[1] SOUTH DAKOTA

SKULL, MANDIBLE, AND SKELETON

Skull with I^2–M^3 (lacking rt. premaxillae), mandible with I_1–M_3, "axis, 3 other cervicals, 6 dorsals	A.M. 1287	From "Cheyenne River, Lower *Oreodon* beds," South Dakota, 1894 Figured (in part) by Osborn, 1910, fig. 106;

[1] Exact localities unknown to present writers.

and 3 centra of others, all lumbar, sacrum, caudals 1–4, 9–tip, both fore limbs complete, pelvis and both hind limbs complete, most ribs of both sides." (w) — Scott, 1913, figs. 136, 204A; O'Harra, 1920, pl. 20, fig. B; Scott, 1940, fig. 133, p. 653

The skull, mandible, scapula, cervical and dorsal vertebrae, and caudals 5–12 of A.M. 594 are mounted in a composite skeleton with the limb elements of A.M. 1287.

The mounted skeleton has been accepted and illustrated by previous authors as a typical example of *M. culbertsonii* without a notation that actually it is a composite mount. The present writers consider the skull, A.M. 594, as representing *culbertsonii*, and that of the second individual, A.M. 1287, as of *M. c. osborni*. There is no apparent difference in the skeletal elements of the species and subspecies.

4 SKULLS AND MANDIBLES

Skull with I^1–M^3 (I^3 br.) and mandible with I_1–M_3 (I_3–P_1 rt.). (w‡)	A.M. 595	Figured by Osborn and Wortman, 1894, fig. 5a; Thorpe, 1937, fig. 7

The above specimen was figured by Osborn and Wortman and by Thorpe as *Merycoidodon culbertsonii*.

Skull with I^1–C/ br. and P^1–M^3 and mandible (attached) with I_1–/C rt. and P_1–M_3. (w+)	A.M. 604	From South Dakota, 1892
Skull with I^1–M^3 (I^1–I^3 rt.) and mandible (attached) with I_1–P_1 rt. and P_2–M_3. (w+)	609	From South Dakota, 1892
Skull with I^1–M^3, mandible with I_1–M_3, and atlas. (w)	610	From South Dakota, 1892

SKULL

Skull with I^1(rt.)–M^3. (w+)	A.M. 1297	From "Cheyenne River," South Dakota, 1894

B. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1½–3 MI. W. OF SHEEP MT. (INDIAN CREEK AREA):

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with I^1–I^2 rt. and I^3–M^3, mandible (attached) with I_2–M_3, partial humerus, pelvis, and vertebrae	(w)	45031
Partial skull with I^1–M^3, mandible (attached) with I_1–M_3, 2 partial scapulae, 2 partial humeri, 2 radii (1 partial), and 2 partial ulnae	(w‡)	45236

4 SKULLS AND MANDIBLES (ATTACHED)

4 partial skulls and mandibles with

I^1–I^2 rt. and I^3–M^3 (M^1–M^3 br.); I_1–M_3	(w)	45223
I^2–M^3; I_1(br.)–M_3	(w‡)	45241
C/(br.)–M^3; I_1–I_2 rt. and I_3–M_3	(w)	49671
I^2–M^3; I_2–M_3	(w)	49673

3 SKULLS

3 skulls with

I^1–M^3	(w‡+)	49675
C/(rt.)–dP^2–M^3(erupt.)	(I)	72257
I^1–I^3 alv. and C/–dP^2–M^2	(I)	72258

FROM 2–2½ MI. W. OF S. END OF SHEEP MT. (HEAD OF INDIAN CREEK):

5 SKULLS AND MANDIBLES

5 partial skulls and mandibles with

P^3–M^3 br.; (attached) P_3–M_3	(w‡)	45033
I^2–C/ rt. and P^1–M^3 (P^3 br.); (attached) P_3–M_3	(M)	45061

		F:A.M.
I^1(rt.)–M^3; I_1–I_2 rt. and I_3–M_3	(w‡+)	45117
C/(rt.)–M^3; P_1(rt.)–M_3	(w)	45228
dP^2–M^2; I_1–/C rt. and P_1–dP_2–M_2	(I)	72255

6 SKULLS

Six partial skulls with

I^1–M^3	(w+)	45116
P^3–M^3 (P^4 br.)	(w)	45154
I^1–M^3	(w+)	49674
I^1–P^2 rt. and P^3–M^3	(w+)	49676
C/(rt.)–M^3	(w‡+)	49768
C/–P^1 rt. and dP^2–M^2 (germ)	(I)	72259

MANDIBLE

Partial mandible with I_1–M_3 (br.) (P_1–P_4 rt. and M_1 br.)	(w+)	72260

FROM W. SIDE OF SHEEP MT. (INDIAN CREEK AREA):

2 SKULLS AND MANDIBLES (ATTACHED)

2 skulls and mandibles with

P^2–M^3; P_1(rt.)–M_3	(w)	45068
I^2–I^3 rt. and C/(br.)–M^3; I_1(rt.)–M_3 (I_2 br.)	(M)	49672

The field data of the above specimen state, "above base of Middle Oreodon," (=oreodont faunal "Zone B"). The bullae of the specimen, however, are typical of those from "Zone A."

FROM COTTONWOOD PASS[1]:

SKULL

Skull with C/(rt.)–M^3	(M)	45074

FOLLOWING FOUR COTTONWOOD PASS LOCALITIES IN REGION OF BIG CORRAL DRAW IN DIVIDE AREA BETWEEN WHITE AND CHEYENNE RIVER DRAINAGES:

SKULL AND SKELETAL ELEMENTS

Skull with I^1(alv.)–M^3, partial scapula, partial radius, and partial ulna	(M)	45032

3 SKULLS

3 skulls with

C/(rt.)–M^3 (M^1 br.)	(w‡+)	49681
C/–M^3	(w‡)	49683
P^1–M^3	(M+)	49684

FROM BIG CORRAL DRAW AREA:

SKULL, MANDIBLE, AND FEMUR

Skull with I^1(alv.)–M^3 (I^2–I^3 rt.), mandible (attached with I_1–I_3 rt. and /C–M_3, and femur	(M)	45242

11 SKULLS AND MANDIBLES

Partial skull with I^1–P^1 rt. and P^2–M^3 and partial mandible (attached) with /C–P_1 rt. and P_2–M_3	(M)	45224
Partial skull with C/(rt.)–M^3 (P^2 br.) and mandible (attached) with I_1–I_3 rt. and /C(br.)–M_3	(w‡)	45226
Skull with I^1–M^3 (I^3 rt. and C/ br.) and partial mandible (attached) with I_1(br.)–M_3 (I_2 br.)	(w)	45244
Partial skull with I^1–M^3 (I^3, C/, and M^3 br.) and partial mandible with I_1–M_3	(w‡)	45248
Partial skull with C/(rt.)–M^3 and partial mandible with I_1–M_3	(w+)	45250

[1] Cottonwood Pass actually is in the divide area between the Cheyenne River and White River drainages.

		F:A.M.
Partial skull with P^1–M^3 and partial mandible with M_2–M_3	(w)	45252
Partial skull with I^1–I^3 rt. and C/(br.)–M^3 and partial mandible (attached) with I_1–/C rt. and P_1–M_3	(w+)	49667
Partial skull with I^1(rt.)–M^3 (C/ br.) and mandible (attached) with I_1(br.)–M_3	(w‡)	49669
Skull with I^3–C/ rt. and P^1–M^3 and mandible with I_1–M_3	(w+)	49678
Inferior, anterior portion of skull with I^1–M^3 and mandible (attached) with I_1–M_3	(w)	49680
Partial skull with I^1–I^3 rt. and C/(br., erupt.)–dP^2–M^2 and mandible (attached) with I_1–dP_2–M_2 (P_1 erupt.)	(I)	72251

SKULL

Partial skull with C/–dP^2–M^3(erupt.)	(I)	72252

FROM BETWEEN BIG AND LITTLE CORRAL DRAWS:

SKULL

Anterior inferior portion of skull with dP^2–M^3(germ)	(I)	72254

FROM LITTLE CORRAL DRAW:

4 SKULLS AND MANDIBLES

Partial skull with I^1–I^3 rt. and C/–M^3 and partial mandible with I_3–/C rt. and P_1–M_3	(w‡+)	45045
Anterior portion of skull with I^3–C/ rt. and P^1–M^3 and partial mandible with P_2–M_3	(w+)	45138
Anterior portion of skull with C/(rt.)–M^3 and partial mandible with P_1–M_3	(w)	45235
Skull with I^1–M^3 and mandible (attached) with I_1–M_3	(w)	49670

SKULL

Partial skull with P^3–M^3	(w)	45145

FROM HEAD OF QUINN DRAW:

2 SKULLS AND MANDIBLES (ATTACHED)

Skull with I^1(br.)–M^3 and mandible with I_1(br.)–M_3 (I_2 br.)	(w)	49686
Partial skull with I^1–M^3 and mandible with I_1–M_3	(w‡)	49769

2 SKULLS

Partial skull with P^2–M^3	(w+)	49770
Partial skull with P^3–M^3	(w+)	49785

MANDIBLE

Partial mandible with I_1(rt.)–M_3	(w‡)	49786

FROM HEAD OF BATTLE CREEK DRAW:

5 SKULLS

5 partial skulls with		
P^1(br.)–M^3(br.)	(w‡)	45035
P^3(br.)–M^3	(w‡)	45049
C/(rt.)–M^3	(w)	45053
I^1–C/ alv. and P^1(rt.)–M^3 (P^2 rt. and P^3 br.)	(M)	72262
I^3(rt.)–dP^2–M^3(germ)	(I)	72263

FROM BATTLE CREEK DRAW:

SKULL

Skull with I^3(rt.)–M^3 (P^1 rt.)	(M+)	45075

FROM E. SIDE OF BATTLE CREEK DRAW:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		F:A.M.
Skull with I^1–M^3 (I^3 rt.), mandible (attached) with I_1(rt.)–M_3, partial ulna, atlas, and vertebrae	(W)	49771

FROM BETWEEN BATTLE CREEK DRAW AND BATTLE CREEK CANYON:

SKULL AND MANDIBLE		
Skull with I^1–M^3 and mandible with I_1(rt.)–M_3	(M+)	45066

B′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1 MI. E. OF COTTONWOOD PASS:

2 SKULLS AND MANDIBLES (ATTACHED)		F:A.M.
Posterior portion of skull with P^4(br.)–M^3 and partial mandible with M_1(br.)–M_3	(W)	45139
Partial skull with C/(rt.)–M^3 and partial mandible with P_2–M_3	(W+)	45048

FROM YELLOW ROOT MEDICINE CREEK AREA:

SKULL AND MANDIBLE (ATTACHED), IMMATURE		
Partial skull with dP^2–M^2 and mandible with dP_2–M_2	(I)	72277

C. FROM CHEYENNE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM N. OF SHEEP MT.:

2 SKULLS AND MANDIBLES (ATTACHED)		
2 skulls and mandibles with		F:A.M.
I^3(rt.)–M^3; P_1–M_3	(W)	45067
I^1(alv.)–M^3; I_1–M_3	(W+)	49767

FROM E. SIDE OF SADDLE HORSE PASS[1]:

SKULL AND MANDIBLE, IMMATURE		
Partial skull with I^2–dP^2–M^2 and mandible (left ramus attached) with I_3(br.)–dP_2(br.)–M_2	(I)	72274

SKULL		
Partial skull with I^1–C/ rt. and P^1–M^3	(W+)	45056

C′. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM MILLER BASIN, CAIN CREEK AREA:

SKULL, MANDIBLE, AND FEMUR		F:A.M.
Partial skull with I^1–C/ rt. and P^1–M^3, mandible (attached) with I_2–/C rt. and P_1(br.)–M_3, and femur	(M)	45207

8 SKULLS AND MANDIBLES		
8 partial skulls and mandibles with		
C/(br.)–M^3; (attached) I_1–/C rt. and P_1–M_3	(W)	45069
C/(rt.)–M^3; (attached) P_1(br.)–M_3	(W)	45118
P^2(br.)–M^3(br.); P_3–P_4 rt. and M_1–M_3	(W‡+)	45165
C/(br.)–M^3; (attached) I_1–/C rt. and P_1(br.)–M_3	(M)	45199
C/–P^1 rt. and P^2–M^3; I_1(rt.)–M_3 (I_2 and I_3 br.)	(M)	45208
C/(br.)–M^3; P_2–M_3	(M)	45211
C/–P^2 rt. and P^3–M^3; P_1–M_3	(M)	45215
P^4–M^3; (attached) M_1–M_3	(M)	45251

[1] Saddle Horse Pass is in the divide area between the Cheyenne River and White River drainages.

5 SKULLS		F:A.M.
5 partial skulls with		
C/–P^1 rt. and P^2(br.)–M^3	(W)	45167
C/–P^1 rt. and P^2–M^3	(M+)	45195
I^1(rt.)–M^3 (I^2–C/ br.)	(M+)	49666
C/–dP^2–M^3(erupt.)	(I)	72269
dP^3(br.)–M^3(germ)	(I)	72270

2 MANDIBLES		
2 partial mandibles with		
P_4–M_3	(W)	72272
I_1–/C rt. and P_1(br.)–M_3	(M+)	72273

FROM BASIN E. OF MILLER BASIN:

SKULL AND MANDIBLE		
Partial skull with I^1–I^2 rt. and I^3–M^3 (C/ and P^2 br.) and mandible with I_1–/C rt. and P_1(br.)–M_3	(W)	45222

4 SKULLS		
4 partial skulls with		
P^2–P^3 br. and P^4–M^3	(W‡+)	45175
C/–P^1 rt. and P^2–M^3	(W)	45220
P^1–P^2 rt. and P^3–M^3	(W)	45253
C/(rt.)–dP^2–M^2(germ) (P^1 alv.)	(I)	72268

FROM ½–2½ MI. E. AND 3 MI. N. OF IMLAY:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with I^3–M^3 and mandible with I_1–I_2 rt. and I_3–M_3	(M+)	45196

3 SKULLS		
Partial skull with C/–P^1 rt. and P^2–M^3	(M)	45070
Skull with I^2–P^1 rt. and P^2–M^3. Figure 1	(M)	45217A
Posterior border of nasals are blunt, and more depth to malar below orbit than in F:A.M. 45217B.		
Skull with I^1–I^3 rt. and C/–M^3. Figure 1	(M)	45217B
Posterior border of nasals pointed. The above two specimens were found associated in the field, and show cited individual variation.		

FROM ¾–1 MI. W. OF IMLAY:

2 SKULLS		
Partial skull with I^1–C/ rt. and P^1–M^3	(M)	45062
Partial skull with C/(rt.)–M^3	(W+)	45076

FROM 1½–2 MI. E. AND ½–3 MI. S. OF IMLAY:

SKULL AND MANDIBLE		
Partial skull with I^1–C/ rt. and P^1–M^3 and partial mandible with P_2–M_3	(M+)	45214

SKULL		
Anterior portion of skull with P^1–P^2 rt. and P^3–M^3	(W)	45166

FROM 1 MI. E. OF IMLAY:

SKULL AND MANDIBLE		
Partial skull with I^3–C/ rt. and P^1–M^3 and partial mandible with M_2(br.)–M_3	(M)	45077

FROM 6–8 MI. W. AND 1–4 MI. N. OF CONATA:

2 SKULLS AND MANDIBLES		F:A.M.
Partial skull with I^2–C/ rt. and P^1–M^3 and partial mandible (attached) with /C(rt.)–M_3 (P_1 br.)	(w)	45036
Partial skull with P^2–P^3 rt. and P^4(br.)–M^3 (M^1–M^2 br.) and partial right ramus with M_2–M_3	(w+)	45097

FROM 6–7 MI. W. AND 1 MI. S. OF CONATA:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with C/(rt.)–dP^2–M^3(germ) and mandible with /C(rt.)–dP_2–M_2	(I)	72275

SKULL		
Partial skull with I^2(alv.)–M^3 (P^3–P^4 erupt., C/ br., dP^4 on right side)	(I)	45201

FROM 7 MI. E. AND 2 MI. N. OF CONATA:

2 SKULLS AND MANDIBLES		
Partial skull with I^2–M^3 and mandible (attached) with I_1–I_3 alv. and /C–M_3	(w‡)	45030
Partial skull with C/–P^1 rt. and P^2–M^3 and partial left ramus with M_1–M_3	(M+)	45042

FROM 1 MI. S. OF CONATA:

SKULL		
Partial skull with I^1–I^3 rt. and C/–M^3	(w+)	45072

FROM NEAR SCENIC (A.M. SPECIMENS COLLECTED BY WALTER GRANGER, ALBERT THOMSON, AND EDWIN COLBERT, 1939 AND 1941):

4 SKULLS AND MANDIBULAR RAMI		A.M.
Skull with I^1–M^3 and mandible (attached) with I_1–I_2 rt. and I_3–M_3 (/C rt.)	(w)	39002
Skull with I^1–M^3 and mandible with I_1–M_3	(w‡+)	39425
Skull with I^2–M^3 and mandible with I_1–M_3	(w)	39426
Partial skull with I^2(br.)–M^3 (I^3 alv., C/ br.) and partial mandible with I_1(rt.)–M_3 (I_2, /C and M_1–M_2 br.)	(w+)	48821

4 SKULLS		
Skull with I^1–I^2 alv. and I^3(rt.)–M^3	(M+)	39414
Skull with I^1(alv.)–M^3 (P^1 rt.)	(M)	39430
Skull with I^1(alv.)–dP^3–M^3(germ)	(I)	39460
Partial skull with C/–P^3 br. and P^4–M^3	(w)	39472

FROM 4½ MI. SE. OF SCENIC:

SKULL		F:A.M.
Anterior portion of skull with P^1(rt.)–M^3	(M)	45040

FROM 4 MI. E. OF SCENIC:

SKULL AND MANDIBLE		
Anterior portion of skull with I^2–C/ br. and P^1–M^3, and partial left ramus with M_1–M_3	(w+)	45162

D. FROM WHITE RIVER DRAINAGE, JACKSON COUNTY, SOUTH DAKOTA

FROM HODGES BASIN, 9 MI. E. OF INTERIOR:

SKULL		F:A.M.
Partial skull with I^2–P^1 rt. and P^2–M^3	(M)	45119

FROM P.U. COLL. LOC. NO. 1014–A2:

SKULL		P.U.
Partial skull with C/(br.)–M^3	(w‡)	12504

E. FROM SLIM BUTTES AREA, HARDING COUNTY, SOUTH DAKOTA

FROM HEAD OF POINT CREEK:

SKULL AND MANDIBLE (ATTACHED)		F:A.M.
Partial skull with I^1–I^3 rt. and C/(br.)–M^3 and mandible with I_1–I_3 and /C–M_3	(w)	49688
SKULL		
Partial skull with I^3–C/ rt. and P^1–M^3	(w‡)	49690

FROM BATTLE MONUMENT AREA:

SKULL AND MANDIBLE (ATTACHED)		
Skull with I^1(rt.)–M^3 and mandible with I_1–M_3	(w‡)	49687

FROM 2 MI. S. OF REVA GAP:

SKULL, IMMATURE		
Partial skull with I^2–C/ rt. and P^1–dP^2–M^3(erupt.)	(I)	49692

F. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM NORTH OF HARRISON (=U.N.S.M. COLL. LOC. SX–6 AND 7):

3 SKULLS AND MANDIBLES		F:A.M.
Skull with I^1(alv.)–M^3 (I^3 and C/ br.) and mandible (attached) with I_1–I_3 rt. and /C–M_3	(w+)	49663
Partial skull with C/–M^3 (P^2–P^3 rt.) and partial mandible with P_1–M_3	(w‡+)	49665
		A.M.
Skull with I^1–M^3 and mandible with I_1(br.)–M_3	(w‡)	1296
Collected in 1894 (exact collecting locality questionable).		

FROM U.N.S.M. COLL. LOC. SX–4:

3 SKULLS AND MANDIBLES		U.N.S.M.
Partial skull with I^1–M^3 and mandible (attached) with I_1–M_3	(w‡)	28093
Anterior portion of skull with I^2–C/ rt. and P^1–M^3, and partial mandible with M_2–M_3	(w+)	28113
Partial skull with dP^3–M^3(erupt.) and partial mandible with I_1–I_2 rt. and I_3–dP_4–M_3 (/C–P_2 br.)	(I)	28145
SKULL		
Partial skull with C/(br.)–dP^2–M^3(erupt.)	(I)	28109

FROM U.N.S.M. COLL. LOC. SX–5:

2 SKULLS		
Partial skull with P^2(br.)–M^3	(w)	28066
Partial skull with C/(rt.)–M^3 (P^3 br.)	(w+)	28276

FROM U.N.S.M. COLL. LOC. SX–12:

SKULL		
Partial skull with I^1–P^1 rt. and P^2–M^3, and partial mandible with I_1–I_3 rt. and /C–M_3 (P_1, M_2–M_3 br.)	(w‡)	28031

FROM MENG RANCH AREA (=U.N.S.M. COLL. LOC. SX–12, 13, AND 14):

SKULL		F:A.M.
Skull with I^2–M^3	(w‡+)	72240

FROM AREA OF U.N.S.M. COLL. LOC. SX–37 AND 38:

SKULL		U.N.S.M.
Partial skull with P^1–M^3	(M)	28080

F′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–17:

SKULL		U.N.S.M.
Partial skull with I^1–I^3 rt. and $C/$–M^3 (P^1 br.)	(w‡+)	28069

FROM U.N.S.M. COLL. LOC. SX–22:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with $C/$(br.)–M^3 (P^1, M^1–M^2 br.) and partial mandible with P_1(br.)–M_3	(w‡)	28028

The anteroposterior measurement of the above M^3 is larger than usual in this species.

FROM U.N.S.M. COLL. LOC. SX–24:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–M^3 and mandible with I_1(rt.)–M_3	(w‡)	28065

FROM U.N.S.M. COLL. LOC. SX–26:

3 SKULLS AND MANDIBLES (ATTACHED)

Skull with I^1–dP^2–M^2 and mandible with I_1–dP_2–M_2	(I)	28622
Skull with I^1–M^3 and mandible with I_1–M_3	(w‡)	28036

The anteroposterior measurement of the above M^3 is longer than usual in this species.

Partial skull with I^1–M^3 and mandible with I_1(rt.)–M_3	(w‡)	28100

SKULL AND MANDIBLE

Partial skull with P^1–M^3 and partial mandible with P_4(br.)–M_3	(w+)	28077

SKULL AND RADIUS

Partial skull with P^1–M^3 (P^2 alv.) and partial radius	(w)	28081

SKULL

Partial skull with $C/$–P^1 rt. and P^2–M^3	(M+)	28468

FROM ¼ MI. W. OF U.N.S.M. COLL. LOC. SX–30:

SKULL AND MANDIBLE, IMMATURE

Skull with I^2(br.)–dP^2–M^3(erupt.) and mandible (attached) with I_1–dP_2–M_3(erupt.)	(I)	28149

FROM U.N.S.M. COLL. LOC. SX–31:

SKULL AND MANDIBLE

Anterior portion of skull with $C/$–M^3 and partial mandible with I_1–M_3	(w‡)	28334

2 SKULLS

Partial skull with P^1(rt.)–M^3	(w)	28083
Partial skull with I^1(rt.)–M^3 (I^2–I^3 alv. and $C/$ br.)	(w+)	28104

FROM U.N.S.M. COLL. LOC. SX–32:

SKULL — U.N.S.M.

Anterior portion of skull with C/(br.)–M^3 . . . (M+) 28283

G. FROM WHITE RIVER DRAINAGE, DAWES COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. 5 MI. N. OF HORN:

SKULL — U.N.S.M.

Partial skull with C/(rt.)–M^3 (P^1–P^2 br. and P^3 alv.) . . . (M) 28101

FROM U.N.S.M. COLL. LOC. No. DW–105:

2 SKULLS

Partial skull with I^1(alv.)–dP^3–M^2 (P^2 rt.) . . . (I) 28119
Partial skull with I^1–I^3 rt. and C/–M^3 . . . (w‡+) 28150

FROM WALTER BRECHT RANCH AREA (=U.N.S.M. COLL. LOC. DW–104):

SKULL, MANDIBULAR RAMUS, AND SKELETAL ELEMENTS — F:A.M.

Partial skull with I^1–I^3 rt. and C/–M^3, right ramus with I_1(rt.)–M_3, tibia, astragalus, and fragments of pes . . . (w‡‡) 72239

SKULL AND MANDIBLE

Partial skull with I^1–M^3 (I^2–I^3 br.) and fragments of mandible with I_1(rt.)–P_2 and M_2–M_3(br.) (I_2–P_1 rt.) . . . (w) 72238

SKULL

Partial skull with I^1–M^3(br.) . . . (w‡+) 72300

FROM 2 MI. N. OF CHADRON (=U.N.S.M. COLL. LOC. DW–105):

SKULL, IMMATURE

Partial skull with C/–P^2 rt. and dP^3(br.)–M^3(erupt.) . . . (I) 72299

H. FROM NORTH PLATTE RIVER DRAINAGE, U.N.S.M. COLL. LOC. SF–101, SCOTTS BLUFF COUNTY, NEBRASKA

SKULL — U.N.S.M.

Partial skull with I^2–P^1 rt. and P^2(br.)–M^3 . . . (w‡) 28072

I. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SEAMEN HILLS AREA:

2 ASSOCIATED SKULLS, MANDIBLES, AND SKELETAL ELEMENTS — F:A.M.

Skull with I^1–M^3 and mandible with I_2(rt.)–M_3 (I_3–/C alv.) . . . (M+) 72246A
Skull with I^3–C/ br. and P^1–M^3 and mandible with I_2–I_3 rt. and /C–M_3 (P_1–P_3 br.) . . . (w‡+) 72246B
4 partial humeri, 2 radii, 2 ulnae (1 partial), partial manus, 3 femora (2 partial), 2 tibiae, astragalus, calcaneum, partial pes, pelvis, and vertebrae . . . 72246A–B

All the above material was found associated in the field. The limb elements are of the same approximate size. Skull F:A.M. 72246A has an acute posterior border of the nasals; skull 72246B is obtuse. This evidence is similar to that in the two associated skulls F:A.M. 45217A and B from South Dakota.

SKULL, MANDIBLE, AND PES, IMMATURE

Partial skull with dP^1(br.)–M^3(erupt.), partial mandible with P_1(rt.)–dP_2(rt.)–M_3 (erupt.), and partial pes . . . (I) 72298

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Skull with I^1–M^3, mandible (attached) with I_3(br.)–M_3, partial scapula, 2 humeri, 2

F:A.M.

radii, 2 ulnae (1 partial), 2 partial manus, 2 femora, 2 partial tibiae, 2 astragali, 2 partial calcanea, 2 partial pedes, pelvis, vertebrae, and ribs . . . . (M+) 49644

A partial humerus and partial manus of a second individual also were found associated with the above specimen. All 3 manus have five digits.

Skull with I^1–M^3, mandible with I_1–M_3, partial humerus, astragalus, partial pes, and vertebrae . . . . (W‡) 49776

The above skull contains two canines on each side.

3 SKULLS AND MANDIBLES

Skull with I^1–I^2 rt. and I^3–M^3, and mandible with I_1–M_3 . . . . (W) 49777
Skull with I^1–M^3 and mandible (attached) with I_1–M_3 . . . . (W+) 49778
Skull with I^3–C/ br. and P^1–dP^2–M^2, and mandible (attached) with I_2–/C rt. and P_1–dP_2–M_2 . . . . (I) 49779

2 SKULLS AND SKELETAL ELEMENTS

Skull with C/–M^3, partial ulna, and atlas . . . . (W) 49780
Partial skull with C/–dP^3–M^3(erupt.), partial scapula, 2 partial humeri, 2 partial radii, partial ulna, and partial femur . . . . (I) 49784

2 SKULLS

Skull with I^1–M^3 . . . . (M+) 49781
Skull with I^1–dP^2–M^3(erupt.) . . . . (I) 49782

FROM EAST OF U. S. HIGHWAY NO. 85:

SKULL AND MANDIBULAR RAMUS

Partial skull with C/–P^1 rt. and P^2–M^3 and partial left ramus with M_1–M_3 . . . . (M) 45084

The anteroposterior measurement of the above M^3 is longer than usually found in this species.

SKULLS

3 partial skulls with
C/–P^1 rt. and P^2–M^3 . . . . (W‡) 45059
C/–P^1 rt. and P^2(br.)–M^3 . . . . (M+) 45108
I^1–M^3 . . . . (W) 45121

FROM AREA NORTH OF NODE:

2 SKULLS, AND MANDIBLES (ATTACHED), AND SKELETAL ELEMENTS

Partial skull with I^1–M^3, mandible with I_1–M_3, radius and partial ulna. . . . . . (W‡+) 49645
Skull with I^2–M^3, mandible with I_1–M_3, and vertebrae . . . . (W+) 49646

5 SKULLS AND MANDIBLES (ATTACHED)

5 skulls and mandibles with
C/–M^3; I_1–I_3 rt. and /C–M_3 . . . . (W‡) 49647
C/–M^3 (P^1 and M^1–M^2 br.); I_1–M_3 (/C br.) . . . . (W‡) 49648
I^1–M^3; I_1–M_3 . . . . (W‡) 49649
I^1–dP^2–M^3(erupt.); I_1–I_3 br. and /C–dP_2–M_3(germ) . . . . (I) 49650
C/(rt.)–dP^2–M^2; I_3–dP_2–M_3(germ) . . . . (I) 72248

SKULL

Partial skull with C/–M^3 (P^1 br.) . . . . (M+) 49651

FROM INDIAN CREEK AREA:

2 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Skull with I^1–M^3, mandible with I_1–M_3, and partial radius . . . . (W+) 49653
Skull with I^1–C/ br. and P^1–M^3 (P^2–P^3 rt.), partial left ramus with /C(br.)–M_3, partial humerus, and partial ulna . . . . (M+) 72247

SKULL AND MANDIBLE — F:A.M.

Skull with I^3–M^3 and mandible with I_1(rt.)–M_3 (P_1 br.) . . . (w+) 49652

MAXILLA, MANDIBLE, AND SKELETAL ELEMENTS

Partial left maxilla with M^1–M^3(br.), partial mandible with M_1–M_3, partial scapula, 2 humeri (1 partial), partial radius, partial ulna, 2 femora, 2 tibiae (1 partial), 2 astragali, 2 calcanea, partial pes, partial pelvis, and vertebrae . . . (w) 49783

FROM SHACK DRAW AREA:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–M^3 (I^2–I^3 and C/ br.) and mandible with I_1–M_3 (P_1 br.) . . . (w+) 45120

SKULL AND SKELETAL ELEMENTS

Partial skull with I^1–I^3 alv. and C/–M^3, partial tibiae, astragalus, manus and pes elements, and vertebrae . . . (w) 49655

2 SKULLS

Skull with I^1–I^2 rt. and I^3–M^3 (C/br.) . . . (w) 45090
Skull with I^2(alv.)–M^3 (C/ br.) . . . (m+) 49656

FROM SPRING DRAW AREA:

2 SKULLS AND MANDIBULAR RAMI

Skull with I^1(alv.)–M^3 (I^2 rt.) and partial left ramus with P_1(alv.)–M_3 (P_2 rt.) . . . (w+) 45058
Partial skull with P^4(br.)–M^3 (M^1–M^2 br.) and partial mandible (attached) with M_1–M_3 . . . (w) 45126

4 SKULLS

4 partial skulls with
C/–P^2 rt. and P^3(br.)–M^3 . . . (m+) 45028
I^1–I^3 alv. and C/(br.)–M^3 . . . (w+) 45106
I^3–P^3 rt. and P^4–M^3 . . . (w‡+) 45122
C/(rt.)–M^3 (P^1 br.) . . . (w‡) 45135

J. FROM NORTH PLATTE RIVER DRAINAGE, 6 TO 8 MILES SOUTHEAST OF DOUGLAS, CONVERSE COUNTY, WYOMING

4 SKULLS AND MANDIBLES — F:A.M.

Skull with I^1–M^3 and mandible with I_1–I_2 rt. and I_3–M_3 . . . (w+) 45109
Partial skull with I^3–M^3 and partial mandible (attached) with /C–M_3 . . . (w) 45172
Skull with C/–M^3 and mandible (attached) with I_3–/C br. and P_1–M_3 . . . (w‡+) 49657
Skull with C/(br.)–dP^2–M^3(germ) and mandible with I_3(br.)–dP_2–M_3(germ) . . . (i) 49659

4 SKULLS

Partial skull with P^2–M^3 . . . (m) 45173
Partial skull with I^1–M^3 . . . (w‡) 49660
Skull with I^1–I^3 alv. and C/(rt.)–M^3 . . . (w‡+) 49661
Skull with I^1–M^3 . . . (w‡) 49774

K. FROM STARK COUNTY, NORTH DAKOTA

FROM 7–10 MI. S. OF SOUTH HEART:

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Skull with I^1–I^3 alv. and C/(br.)–M^3, mandible with I_1–M_3, partial scapula, humerus, radius, partial ulna, partial manus, 2 partial femora, 2 partial tibiae, astragalus, partial pes, partial pelvis, and vertebrae . . . (m) F:A.M. 49696

The dentition of the above specimen shows a mature stage of wear, yet some of the epiphyses on the ends of the limbs are not fused. The femur is exceptionally long.

Partial skull with P^1–M^3, mandible (attached) with P_2(rt.)–M_3, partial scapula, 2 humeri (1 partial), radius, partial ulna, partial manus, and vertebrae	(M)	F:A.M. 49697

14 SKULLS AND MANDIBLES

Skull with I^1–M^3 and mandible with I_1–M_3	(w‡$^+$)	49698
Partial skull with C/(br.)–M^3 and partial mandible (attached) with M_1–M_3	(w+)	49699
Right side of skull with C/–M^3 (M^1 br.) and partial mandible (attached) with I_1(rt.)–M_3	(w+)	49700
Partial skull with C/(br.)–M^3 (P^1 br.) and partial mandible with I_1–I_3 rt. and /C–M_3	(w+)	49701
Partial skull with P^1–M^3 and partial mandible (attached) with P_1(rt.)–M_3	(w+)	49702
Partial right side of skull with C/–P^3 rt. and M^2–M^3 br., and partial mandible with I_1(rt.)–M_3	(w+)	49703
Anterior portion of skull with C/(rt.)–M^3 and partial mandible with P_1(rt.)–M_3	(w‡)	49704
Anterior portion of skull with P^2–M^3 and partial mandible with P_1(rt.)–M_3 (P_2 br.)	(w‡)	49705
Partial skull with C/–M^3 and partial mandible with P_2–M_2 br.	(M)	49706
Cranium and partial right ramus with P_1(rt.)–M_2(rt.) (M_1 rt.)	(w+)	49707
Premaxilla, left and right maxilla with I^2–C/ and P^3–M^3, and partial mandible with M_1–M_3	(w+)	49708
Anterior portion of skull with dP^3–M^1 and partial mandible with I_1(alv.)–P_3(br.) and dP_4–M_2(germ) (I_3 and /C rt.)	(I)	49709
Skull with I^1–M^3 and mandible (attached) with I_1–M_3	(M)	72243
Partial skull with I^1–C/ rt. and P^1–M^3, and mandible with I_1–M_3	(w‡$^+$)	72244

SKULL AND SKELETAL ELEMENTS

Partial skull with I^1–M^3 (I^2 and C/ rt.), partial humerus, partial radius, and ulna	(w+)	49710

7 SKULLS

7 partial skulls with		
C/(rt.)–M^3 (P^1–M^2 br.)	(w+)	49711
M^1–M^3	(M+)	49712
I^1–M^3	(w)	49713
P^2–dP^3–M^3(erupt.)	(I)	49714
P^2–M^3	(w‡)	49715
I^2–I^3 alv. and C/(br.)–M^3 (P^1 rt.)	(w‡)	49775
I^3–dP^2–M^2	(I)	72245

3 MANDIBULAR RAMI

Partial mandible with I_2–M_3	(w‡)	49717
Partial mandible with I_1(alv.)–M_3 (P_2–P_3 alv.)	(w‡$^+$)	49718
Partial left ramus P_1(rt.)–M_2(rt.) (P_3–P_4 br. and M_1 alv.)	(w+)	49720

SKELETAL ELEMENTS

Partial radius, partial ulna, 2 partial femur, partial pelvis, metapodial, and vertebrae		72054

FROM 13 MI. S. AND 8 MI. W. OF DICKINSON:

SKELETAL ELEMENTS

Partial scapula, 2 humeri, 2 radii, 2 ulnae, partial manus, 2 femora, 2 tibia, astragalus, 2 calcanea, partial pes, vertebrae, and ribs		72055

L. FROM CEDAR CREEK SOUTH PLATTE RIVER DRAINAGE, LOGAN COUNTY, COLORADO (COLLECTED BY BARNUM BROWN, 1898)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P^2–M^3, partial mandible with P_3–P_4 rt. and M_1–M_3 (M_2 br.), partial radius, partial ulna, and vertebrae	(w)	A.M. 8914

2c. Geologic Variety from Chadron "Zone C"[1]

The following specimens are from oreodont faunal "Zone C" of the Chadron, within 15 feet of the Brule-Chadron contact. As is typical of specimens from the upper Chadron deposits, they do not differ noticeably from examples from the Lower Orella Member of the Brule Formation representing the same phylum.

EXAMPLE

Partial skull with P^1–M^3 and partial mandible with P_1–P_2 rt. and P_3–M_3. (w‡+)	U.N.S.M. 28200	From faunal "Zone C" of Chadron Formation, below "Purple White Layer," White River Drainage, U.N.S.M. Coll. Loc. SX-24, Sioux County, Nebraska; collected by C. Bertrand Schultz and associates, 1938

ADDITIONAL EXAMPLES FROM (M) DAWES COUNTY, NEBRASKA; AND (N) NIOBRARA COUNTY, WYOMING

M. FROM WHITE RIVER DRAINAGE, BRECHT STOCK DAM AREA (=U.N.S.M. COLL. LOC. DW-104), DAWES COUNTY, NEBRASKA (COLLECTED BY MORRIS F. SKINNER AND ASSOCIATES, 1953)

SKULL		F:A.M.
Fragments of anterior portion of skull with I^3–C/ rt. and P^1–M^3 (P^3 absent) . . .	(w)	72314
MANDIBULAR RAMUS		
Partial left ramus with M_1–M_3	(w+)	72315

N. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SOUTHEAST END OF SEAMEN HILLS, NIOBRARA COUNTY, WYOMING (COLLECTED BY CHARLES H. FALKENBACH AND ASSOCIATES, 1953)

SKULL		F:A.M.
Fragments of skull with P^3–M^3(br.)	(w)	49763

3. **Merycoidodon macrorhinus** (Douglass)

From "Zone A" of the Brule Formation, Broadwater County, Montana

Oreodon robustum DOUGLASS, 1901b, p. 264 (*robustum* preoccupied).

Merycoidodon robustus (Douglass): TROUESSART, 1905, p. 667.

Oreodon macrorhinus DOUGLASS, 1903, p. 163, fig. 8.

Merycoidodon macrorhinus: DOUGLASS, 1907a, p. 821. THORPE, 1937, p. 58, fig. 24, pl. 2, figs. 7-8.

CHARACTERS

SKULL: Within size range of examples of *M. culbertsonii;* characters similar to those of that species except for the following differences: lacrimal fossa with tendency to be larger and deeper, nasals wider transversely, muzzle wider (wider than examples of any species of the Merycoidodontinae from "Zone A"); postglenoid process more massive (more like examples of *Paramerycoidodon* in this respect).

MANDIBLE: (Unknown).

DENTITION: Similar to examples of *M. culbertsonii;* P^2 with weak anterior intermediate crest (P^2 only complete premolar present in holotype).

LIMBS: (Unknown).

MEASUREMENTS: Table 1 (p. 35).

ILLUSTRATIONS: Figures 1, 3.

DISCUSSION

Douglass[2] originally described this form as *"Oreodon robustum,"* not realizing that the specific name was preoccupied. Later Douglass[3] stated: "In my paper [1901] . . . I described a species of *Oreodon robustum.* I knew that the name had been given by Leidy to an individual belonging to *O. culbertsonii,* but considered the name still available. I propose for it the specific name *macrorhinus."*

Still later Douglass[4] reported, "It may be that *Merycoidodon macrorhinus* may turn out

[1] See discussion, p. 412.

[2] 1901b, p. 264.

[3] 1903, p. 163.

[4] 1907a, p. 821.

to be a very robust variety or individual of *Merycoidodon culbertsonii*." This was the first reference of *macrorhinus* that assigned it to the genus *Merycoidodon*.

Thorpe's[1] conclusions were similar to those of Douglass; he stated, ". . . I should consider it a valid species for the present. We may think of it as a robust species (or subspecies), living in the general region of western Montana, but not far removed from the Great Plains *M. culbertsonii*, perhaps representing a localized variant of that species."

Scott[2] pointed out the difference between *Merycoidodon culbertsonii* and *M. macrorhinus*, which are mainly valid, and concluded, "Montana mammals of the White River age are so generally different from those of South Dakota and Nebraska, as to suggest a slight difference in time." This is partially due to the fact that most of the Montana Oligocene deposits are equal in age to "Zone B" of the Chadron. The deposits of equal age in Nebraska and Wyoming (with the exception of the Bates Hole of Wyoming) are almost non-fossiliferous.

The types of *M. macrohinus* and *Otionohyus* (*Otarohyus*) *helenae* came from the Tosten area of Montana, the former from deposits approximately equal in age to "Zone A" of the Brule, and the latter from "Zone C." (See discussion of the occurrences of *macrorhinus* and *helenae*, p. 131.)

The dentition of *M. macrorhinus* is not distinguishable from that of *M. culbertsonii*. P^2 exhibits a weak anterior intermediate crest, and P^1 and P^3 are damaged to the extent that it is impossible to tell if the crests were present or not. Thorpe[3] described the dentition as follows: "The anterior three premolars have large posterior basins and well-developed posterior crescents, with a reduction of the anterior crescent. The anterior and posterior crests are strong, and the median crest is very weak or absent [this would depend on the age of the individual]. There are two tiny anterior pits separated by a weak antero-intermediate crest. P^4 has a strong internal cingulum and no anteroexternal pit." P^4 does possess a cingulum, but this is a variable character within a species.

The form is here retained as a full species, based primarily on the exceptionally wide muzzle. This could be individual variation. However, no example of *M. culbertsonii* possesses a muzzle as robust as that of the holotype of *M. macrorhinus*.

One specimen is here listed:

HOLOTYPE

Partial skull with I^1(alv.)–M^3(br.) (I^2 rt., I^3 alv., P^1 and P^3 br.). (w)	C.M. 767	From oreodont faunal "Zone A" of the Brule Formation, near Toston, Broadwater County, Montana; collected by Earl Douglass, 1898 Figured by Douglass, 1903, fig. 8; Thorpe, 1937, fig. 24, pl. 2, figs. 7–8 This report, figures 1, 3

IA. MERYCOIDODON (ANOMERYCOIDODON), NEW SUBGENUS

SUBGENOTYPE: *Merycoidodon* (*Anomerycoidodon*) *dani*, new species.

DESCRIPTION

SKULL: Small to medium in size; dolichocephalic; basal lengths ranging from 190 to 211 mm., widths from 106 to 140 mm.; characters similar to those of *Merycoidodon* except for smaller and shallower lacrimal fossa, and inflated auditory bulla with more variation in depth and prominence of hyoidal groove (groove virtually lost in examples from "Zone D" of the Brule).

MANDIBLE: Similar to examples of *Merycoidodon*, but somewhat more robust.

DENTITION: Within the variation found in examples of *Merycoidodon*; P^1–P^3 each with a weak anterior intermediate crest.

LIMBS: Within the variation found in examples of *Merycoidodon*.

MEASUREMENTS: Tables 2 and 7 (pp. 74 and 146).

ILLUSTRATIONS: Figures 4–6, 51 (skulls, mandibles, and dentitions), 19–23 (limbs).

[1] 1937, p. 59.
[2] 1940, p. 676.
[3] 1937, p. 58.

TABLE 2

Merycoidodon (Anomerycoidodon), New Subgenus, and *Merycoidodon (Blickohyus)*, New Subgenus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*M. (A.) dani*, new species — Holotype F:A.M. 72132	*M. (A.) lambi*, new species — Holotype F:A.M. 72139	*M. (B.) galushai*, new species — Holotype F:A.M. 45279	*M. (B.) lynchi*, new species — Holotype F:A.M. 45297
Stage of wear of teeth	(w)	(w)	(w‡)	(M+)
Length (incl. supraoccipital crest and incisors)	219	238.5	((205))	((220))
Basal length (from anterior notch of foramen magnum to posterior base of I^1	194	201	((182))	((192))
Width (max.)	((110))	121	((103))	(115)
Width of brain case (max.)	64	58.5	53	58.5
Width, interorbital (min.)	53	51	50.5	50
Distance from anterior rim of orbit to anterior base of C/	82	81.5	82.5	77.5
Distance from anterior rim of orbit to supraoccipital crest	(144)	153	—	((140))
Length of nasals	(86)	(75)	—	
Width of muzzle at infraorbital foramina	53.5	55	46	48.5
Width across canines	((26))	29	—	—
Length, C/–M^3 incl.	109	110	102	111
Length, P^1–M^3 incl.	92.5	92.5	90.5	99
Length, P^1–P^4 incl.	45.5	46	46	49
Length, M^1–M^3 incl.	48.5	47	47.5	52
Width of M^3 (max.)	19	20	20	21.5
Depth of malar below orbit	16.5	16.5	16.5	17
MANDIBULAR RAMUS				
Length (max., incl. incisors)	(180)	185	((156))	—
Length /C–condyle incl.	160	(163)	—	—
Depth of jaw under coronoid	—	87.5	—	—
Depth of jaw below anterior edge of M_3	31.5	45	35	—
Length, /C–M_3 incl.	113.5	((108))	(92)	—
Length, P_1–M_3 incl.	102.5	100.5	(89)	—
Length, P_1–P_4 incl.	48	48.5	39	47
Length, M_1–M_3 incl.	54	53.5	50	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

Discussion

The skulls of the new subgenus, *Merycoidodon (Anomerycoidodon)*, differ primarily from those of the genus by possessing inflated auditory bullae. Actually, the subgeneric line is a continuation of the *Merycoidodon* phylum (from the Chadron and oreodont faunal "Zone A" of the Brule), but with well-inflated bullae, which are slightly larger in the later stages of the geological sequence (=zones "B" through "D" of the Brule). The limb elements from the various Oligocene horizons, however, show very little variation in size. Unfortunately there are no readily obtainable examples from "Zone C" of the Brule.

There is much individual variation in the skulls, as was noted in *Merycoidodon,* i.e., in width and degree of robustness. This may indicate sex variation, with the lighter-skulled individuals representing the females.

The proposed sequence of the species of *Merycoidodon* (*Anomerycoidodon*) is as follows: *M.* (*A.*) *dani* from "Zone B" of the Brule and *M.* (*A.*) *lambi* from "Zone D" of the Brule ("Zone C" form unknown).

DISTRIBUTION

Two species of *Merycoidodon* (*Anomerycoidodon*) are known from the middle and upper Oligocene (oreodont faunal zones "C" and "D" of the Brule Formation) of Nebraska, North Dakota, and South Dakota. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

Two species of *Merycoidodon* (*Anomerycoidodon*) from six Brule localities are here recorded:

1. *Merycoidodon* (*Anomerycoidodon*) *dani,* new species, from Stark County, North Dakota; referred remains from Jackson, Shannon, and Pennington counties, South Dakota; and Sioux County, Nebraska. (Oreodont faunal "Zone B" of Brule.)

HOLOTYPE: Skull and mandible, F:A.M. 72132. Figures 4–6, 51.

2. *Merycoidodon* (*Anomerycoidodon*) *lambi,* new species, from Jackson County, South Dakota; referred remains from Shannon and Washabaugh counties, South Dakota. ("Zone D" of Brule.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 72139. Figures 4–6, 19–23, 51.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MERYCOIDODON (ANOMERYCOIDODON)

TOTAL AVAILABLE SPECIMENS: 34[1]

1. Merycoidodon (Anomerycoidodon) dani,[2] new species

From "Zone B" of the Brule Formation, Stark County, North Dakota; referred remains from Jackson, Shannon, and Pennington counties, South Dakota; and Sioux County, Nebraska

DESCRIPTION

SKULL: Approximate size of examples of *Merycoidodon culbertsonii;* smaller than those of *M.* (*A.*) *lambi;* bulla much more inflated than in examples of *M. culbertsonii;* bulla less inflated and with more noticeable hyoidal pit than those of *M.* (*A.*) *lambi.* (See subgeneric description.)

MANDIBLE: Similar to examples of *M. culbertsonii.* (See subgeneric description.)

DENTITION: Similar to examples of *M. culbertsonii;* P^1–P^3 each with moderately weak anterior intermediate crest; lighter than examples of *M.* (*A.*) *lambi.* (See subgeneric description.)

LIMBS: Similar to examples of *Merycoidodon culbertsonii* and *M.* (*A.*) *lambi.* (See subgeneric characters.)

MEASUREMENTS: Tables 2 and 7 (pp. 74 and 146).

ILLUSTRATIONS: Figures 4–6, 20–23, 51.

DISCUSSION

Examples of *Merycoidodon* (*Anomerycoidodon*) *dani* differ greatly from those of *M. culbertsonii* in having greatly expanded bullae, and differ from those of *M.* (*A.*) *lambi* in having slightly smaller bullae.

There are three specimens (F:A.M. 45262, 72138, and 45266) referred to this species which differ from the rest of the examples in that they possess somewhat smaller bullae and have decidedly more prominent hyoidal grooves. Perhaps the difference can be attributed to individual variation, or perhaps the material represents another phylum derived from *Merycoidodon culbertsonii osborni.* (See discussion, p. 34, for the suggestion that *M. culbertsonii* and *M. c. osborni* may represent two separate phyla.)

The holotype of *M.* (*A.*) *dani* lacks skeletal elements. The referred specimen, F:A.M. 72138, however, consists of a skull and mandible with associated limbs. The latter skeletal elements are figured for comparison with those

[1] Includes 33 F:A.M. specimens and 1 U.N.S.M. specimen.

[2] Named in honor of Daniel Krochak, former preparator and field assistant of the Frick Laboratory.

of other species. It should be noted that the skull of the referred specimen has smaller bullae than the holotype.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1938, 1945, 1950; and the U.N.S.M. example, by C. Bertrand Schultz and associates, 1937.

Sixteen specimens are here recorded:

HOLOTYPE

Skull with I^1(rt.)–M^3 and mandible with I_1(rt.)–M_3. (w)	F:A.M. 72132	From oreodont faunal "Zone B" of Brule Formation, 23′ below "white marker" in nodular layer, 13 mi. S. and 8 mi. W. of Dickinson, Stark County, North Dakota; collected by Ove Kaisen, Leonard Nelson, Morris F. Skinner, and Morris F. Skinner, Jr., 1945 Figures 4–6, 51

REFERRED FROM (A) JACKSON, (B) SHANNON, AND (C) PENNINGTON COUNTIES, SOUTH DAKOTA, AND (D) SIOUX COUNTY, NEBRASKA

A. FROM WHITE RIVER DRAINAGE, NORBECK PASS AREA,[1] JACKSON COUNTY, SOUTH DAKOTA

FROM ½–1 MI. E. OF NORBECK PASS:

SKULL AND MANDIBLE (ATTACHED)		F:A.M.
Partial skull with I^3–M^3(br.) and mandible with I_1–I_3 rt. and /C–M_3	(w+)	72102
3 SKULLS		
Partial skull with C/–P^1 rt. and P^2–M^3	(w‡+)	72134
Partial skull with C/(rt.)–M^3 (P^2 br.)	(w+)	72135
Partial skull with dP^3(br.)–M^3	(−M)	72136

FROM NORBECK PASS:

SKULL		
Skull with I^1(rt.)–M^3 (I^2 br.)	(M+)	72133

B. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM E. SIDE OF HARNEY SPRINGS RANGE IN SPRING CREEK DRAINAGE, SE. OF S. END OF SHEEP MT.:

4 SKULLS AND MANDIBLES		F:A.M.
Partial skull with P^1–M^3 (P^3–P^4 br.) and mandible with /C–M_3	(w‡)	45259
Partial skull with P^3–M^3 and partial mandible with I_1–M_3 (M_1–M_2 br.)	(w‡)	45260
Partial skull with P^2–M^3(br.) (P^4–M^2 br.) and partial mandible (attached) with I_1–P_3 rt. and P_4–M_3	(w‡)	45360
Portions of skull with P^3–M^3 and partial mandible with I_1–/C rt. and P_1–M_3	(w)	72137
SKULL		
Partial skull with I^3–C/ rt. and P^1–M^3	(w‡)	45266

FROM S. END OF SHEEP MT.:

SKULL AND MANDIBLE		
Fragments of skull with I^2–P^2 rt. and P^3–M^3 (M^1 br.) and partial mandible with I_2–P_3 rt. and P_4(br.)–M_3	(w)	72236

B′. FROM CHEYENNE RIVER DRAINAGE, ½ MILE NORTH OF COTTONWOOD PASS (IN BIG CORRAL DRAW), SHANNON COUNTY, SOUTH DAKOTA

The following three specimens (F:A.M. 45262, 72138, and 45266) differ from

[1] The Norbeck Pass area is on the divide between the White River and Bad River drainages, and located along the Jackson and Pennington county line.

the holotype of *M.* (*A.*) *dani* in possessing bullae with more prominent hyoidal grooves. This difference is considered as individual variation.

FROM ½ MI. N. OF COTTONWOOD PASS:

SKULL		F:A.M.
Partial skull with C/–P^1 rt. and P^2–M^3	(w+)	45262

C. FROM CHEYENNE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM 2 MI. S. OF SCENIC:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		F:A.M.
Partial skull with P^3–M^3, partial mandible with M_2(br.)–M_3, partial scapula, partial humerus, 2 radii (1 partial), partial ulna, partial femur, tibia, astragalus, calcaneum, 2 partial metapodials, partial pelvis, and vertebrae. Figures 20–23 (in part)	(w)	72138

FROM N. END OF SHEEP MT.:

SKULL		
Anterior portion of skull with I^1–P^2 br. and P^3–M^3.	(w+)	45265

D. FROM AREA OF U.N.S.M. COLL. LOC. SX–17 and 18, WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Skull with I^2–I^3 rt. and C/–M^3 and mandible with I_1–/C br. and P_1–M_3	(w‡+)	28061

2. Merycoidodon (Anomerycoidodon) lambi,[1] new species

From "Zone D," Brule Formation, Jackson County, South Dakota; referred remains from Shannon and Washabaugh counties, South Dakota

DESCRIPTION

SKULL: Largest of the subgenus; lacrimal fossa smaller and shallower than in examples of *M.* (*A.*) *dani;* auditory bulla lacking groove for hyoid [groove present in examples of *M.* (*A.*) *dani*]; postglenoid process more robust and more expanded anteroposteriorly than other examples of subgenus. (See subgeneric characters.)

MANDIBLE: Mandibular ramus deeper than examples of *M.* (*A.*) *dani.* (See subgeneric characters.)

DENTITION: Molar-premolar series most robust of subgenus, lighter than examples of *P.* (*B.*) *major,* especially premolars; P^1–P^3 each with moderately weak anterior intermediate crest. (See subgeneric description.)

LIMBS: Similar in length to examples of *Merycoidodon culbertsonii* and *Paramerycoidodon* (*Barbourochoerus*) *major;* slightly less robust than in the latter species, and slightly more so than in *M. culbertsonii.*

MEASUREMENTS: Tables 2 and 7 (pp. 74 and 146).

ILLUSTRATIONS: Figures 4–6, 19–23, 51.

DISCUSSION

Remains of *Merycoidodon* (*Anomerycoidodon*) *lambi* represent the latest geologic occurrence of the generic-subgeneric phylum. The skulls are larger and possess more rounded and greatly inflated bullae than the smaller (minute) bullae of examples of *M. culbertsonii.* The degree of individual variation in this assemblage is less than that found in *M. culbertsonii.* The suggested sex variation present in *P.* (*B.*) *major* (with narrower skulls representing female examples) is not observed in *M.* (*A.*) *lambi.*

The holotype contains large exoccipital vacuities above the paroccipital process. These are similar to those found in examples of the Desmatochoerinae from post-Brule deposits. Other examples of *M.* (*A.*) *lambi* have deep pits with foramina in place of the vacuities. In this instance the vacuity is not considered a diagnostic character. Similar vacuities, however, are found in all specimens of the Desmatochoerinae, as previously mentioned.

It is of interest that example F:A.M. 72124

[1] Named in honor of Alan Lamb, who assisted Morris F. Skinner in making the oreodont collections in 1953.

contains M^3's that have decidedly reduced posterior lobes. The reduction of the lobes is more noticeable on the right side than on the left (see fig. 5). A similar but less pronounced reduction of M^3 is noted in a referred example of *Paramerycoidodon* (*Barbourochoerus*) *bacai*, U.N.S.M. 28469 (p. 178, fig. 9).

The F:A.M. specimens were collected by Morris F. Skinner and associated, 1938–1940, 1945, 1950.

Twenty specimens are here recorded:

HOLOTYPE

Skull with I^1(br.)–M^3, mandible with I_1–M_3, partial scapula, 2 partial humeri, 2 radii (1 partial), 2 partial ulnae, partial manus, 2 femora, 2 tibiae, astragalus, calcaneum, partial pes, pelvis, vertebrae, and ribs. (w)	F:A.M. 72139	From oreodont faunal "Zone D" of Brule Formation, 25′ above base of "*Leptauchenia* beds," 2 mi. W. of Cedar Pass, White River drainage, Jackson County, South Dakota; collected by Morris F. Skinner and associates (Ove Kaisen, Leonard Nelson, and Morris F. Skinner, Jr.), 1945 Figures 4–6, 19–23, 51

REFERRED FROM (A) JACKSON, (B) SHANNON, (C) WASHABAUGH COUNTIES, AND (D) GENERAL AREA, SOUTH DAKOTA

A. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA,[1] JACKSON COUNTY, SOUTH DAKOTA

FROM ¼–1 MI. E. OF CEDAR PASS:

SKULL AND MANDIBLE		F.A.M.
Skull with P^1–M^3 and partial mandible with I_2–P_2 rt. and P_3–M_1	(M+)	72097
SKULL		
Partial skull with P^4(br.)–M^3	(w‡)	72098

FROM 1 MI. NE. OF CEDAR PASS:

SKULL		
Partial skull with I^1–M^3	(M+)	72100

FROM ½ MI. W. OF CEDAR PASS:

SKULL		
Partial skull with M^1–M^3	(w)	72099

B. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM SE. OF SHEEP MT.:

SKULL AND MANDIBLE		F:A.M.
Partial skull with I^1–I^2 alv. and I^3–M^3 and mandible (attached) with I_1–/C rt. and P_1–M_3	(w‡)	72084

FROM SE. OF COTTONWOOD PASS:

SKULL		
Partial skull with C/–dP^1 br. and dP^2–M^1	(I)	72234

B′. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM SW. SIDE OF SHEEP MT.:

2 SKULLS AND MANDIBLES (ATTACHED)		F:A.M.
Skull with I^1(br.)–M^3 (C/ br.) and mandible with P_2–M_3	(M+)	45295
Skull with I^2–C/ rt. and P^1–M^3 and mandible with P_2–P_3 and M_2–M_3	(w+)	72093

[1] The Cedar Pass area is in the divide region between the White River and Bad River drainages.

FROM HEAD OF W. BIG CORRAL DRAW:

SKULL AND MANDIBLE

		F:A.M.
Inferior, anterior portion of skull with C/(rt.)–M^3 (P^1–P^2 br.) and partial mandible with I_1–M_3 (/C–P_1 br.)	(w‡⁺)	45287

FROM DIVIDE BETWEEN BIG CORRAL DRAW AND COTTONWOOD CREEK:

SKULL

Anterior portion of skull with I^1–I^3 alv. and C/(rt.)–M^3	(w)	72092

FROM HIGH DIVIDE IN VICINITY OF HEAD OF E. FORK OF BIG CORRAL DRAW:

SKULL

Partial skull with I^1–C/ alv. and P^1–M^3	(w‡)	72128

C. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM E. BRANCH OF RED WATER CREEK:

2 SKULLS

		F:A.M.
Partial skull with I^1–I^3 alv. and C/–M^3 (P^1 absent)	(M)	72105
Partial skull with C/–M^3. Figure 5	(w+)	72124

On the above skull the distance is greater posterior to the dental series than on other examples of the species. The figure illustrates the unique M^3, which lacks the posterior internal lobe on the left side. There is, however, a vestigial lobe on the right side.

FROM E. SIDE OF POTATO CREEK AREA:

SKULL AND MANDIBLE

Skull with I^3(alv.)–M^3 and mandible with P_1(br.)–M_3	(w+)	72120

2 SKULLS

Partial skull with C/–P^1 br. and P^2–M^3	(M+)	72107
Partial skull with C/–M^3	(w‡)	72108

FROM HAY CREEK AREA:

SKULL AND MANDIBLE (ATTACHED), IMMATURE

Partial skull with C/–dP^2–M^2(erupt.) and mandible with P_1–dP_2–M_2(germ)	(I)	72140

D. FROM GENERAL AREA, SOUTH DAKOTA, 1892

SKULL AND MANDIBLE

		A.M.
Partial skull with C/(br.)–M^3 and mandible with P_2(br.)–M_3	(w‡)	617

MANDIBLE

Mandible with I_1(br.)–M_3	(w)	618

IB. MERYCOIDODON (BLICKOHYUS),[1] NEW SUBGENUS

SUBGENOTYPE: *Merycoidodon* (*Blickohyus*) *lynchi*, new species.

DESCRIPTION

SKULL: Small size; dolichocephalic; basal lengths ranging from 182 to 205 mm., widths from 103 to 140 mm.; characters similar to those of *Merycoidodon* except for posterior portion of skull foreshortened, and bulla inflated; characters similar to those of *M.* (*Anomerycoidodon*) except for smaller size of skull, posterior portion of skull foreshortened, and bulla shorter anteroposteriorly.

MANDIBLE: Characters similar to those of *Merycoidodon* and *M.* (*Anomerycoidodon*) except for smaller size.

DENTITION: Characters similar to those of

[1] Named in honor of the late John C. Blick, who for many years helped to bring the large Frick Laboratory collection together. He was a good personal friend of both the present writers.

Merycoidodon and *M.* (*Anomerycoidodon*) except for the following: series more robust, length of series greater (skull shorter, but dental series longer than examples of mentioned genus and subgenus).

LIMBS: Moderately robust; within size range of examples of *M. culbertsonii.*

MEASUREMENTS: Tables 2 and 7 (pp. 74 and 146).

ILLUSTRATIONS: Figures 4–6, 52 (skulls, mandibular rami, and dentitions), 19–23 (limb elements).

DISCUSSION

The phylogenetic line represented by *Merycoidodon* (*Blickohyus*) is recorded from oreodont faunal zones "C" and "D" of the Brule. The comparison of *M.* (*B.*) *lynchi* and *M.* (*Anomerycoidodon*) *lambi,* both from "Zone D" of the Brule, shows that the skull of the former is the smaller, but the cheek teeth, P^1–M^3, are longer. The skull of *M.* (*B.*) *galushai* from "Zone C" of the Brule is shorter, and the dentition is approximately the same length as that of *M.* (*A.*) *dani* from "Zone B" of the Brule. Although the skulls of the subgenus *M.* (*Blickohyus*) are shorter and narrower than most examples of *Paramerycoidodon* (*Barbourochoerus*) *major* that were found in the same geologic deposits, the dentitions are almost as long but less robust than in examples of the latter species.

The proposed sequence of the species of *Merycoidodon* (*Blickohyus*) is as follows: *M.* (*B.*) *galushai* from "Zone C" of the Brule, and *M.* (*B.*) *lynchi* from "Zone D" of the Brule.

The F:A.M. specimens were collected by Morris Skinner and associates.

DISTRIBUTION

Two species of *Merycoidodon* (*Blickohyus*) are known from upper Oligocene (zones "C" and "D" of the Brule Formation) of Colorado, Nebraska, and South Dakota. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

Two species of *Merycoidodon* (*Blickohyus*) from 14 Oligocene localities are here recorded:

1. *Merycoidodon* (*Blickohyus*) *galushai,* new species, from Jackson County, South Dakota. (Oreodont faunal "Zone C" of Brule.)

HOLOTYPE: Partial skull and partial mandible, F:A.M. 45279. Figures 4–6, 52.

2. *Merycoidodon* (*Blickohyus*) *lynchi,* new species, from Pennington County, South Dakota; referred remains from Jackson and Washabaugh counties, South Dakota; Sioux County, Nebraska; and Colorado. ("Zone D" of Brule.)

HOLOTYPE: Skull and partial mandible, F:A.M. 45297. Figures 4–6, 52.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MERYCOIDODON (BLICKOHYUS)

TOTAL AVAILABLE SPECIMENS: 29[1]

1. Merycoidodon (Blickohyus) galushai,[2] new species

From "Zone C" of the Brule Formation, Jackson County, South Dakota

DESCRIPTION

SKULL: Approximately same size as examples of *M.* (*B.*) *lynchi,* but differing from that species in possessing slightly larger orbit, larger and deeper lacrimal fossa, less inflated muzzle, smaller bulla with more prominent hyoidal groove and pit. (See subgeneric description.)

MANDIBLE: Shallower and lighter than examples of *M.* (*B.*) *lynchi.* (See subgeneric description.)

DENTITION: Premolars slightly smaller; P^2 and P^3 each with moderately strong anterior intermediate crest, longer than examples of *M.* (*B.*) *lynchi.* (See subgeneric description.)

LIMBS: (Unknown).

MEASUREMENTS: Table 2 (p. 74).

ILLUSTRATIONS: Figures 4–6, 52.

DISCUSSION

The holotype is incomplete, but it is the better of the two examples of the species. It is impor-

[1] Includes 27 F:A.M. and 2 U.N.S.M. specimens.

[2] Named in honor of Ted Galusha, a collector for the Frick Laboratory for many years.

tant, however, because of its geologic occurrence ("Zone C" of the Brule), and its characters suggest a link with the *Merycoidodon-M.* (*Anomerycoidodon*) phylum. Examples of this species seem to have been ancestral to those of *M.* (*B.*) *lynchi* from "Zone D" of the Brule. Thus it represents a separate phylum, but is closely related to the *Merycoidodon* line, branching off perhaps during the time of faunal "Zone B" or "C" of the Brule. The dentition is more robust than typical examples of the *Merycoidodon* (*Anomerycoidodon*), but lighter than those of *Paramerycoidodon.*

Two specimens are here recorded:

HOLOTYPE

Partial skull with I^2–C/ rt. and P^1(br.)–M^3 and partial mandible with /C–P_1 rt. and P_2–M_3. (w‡)	F:A.M. 45279	From oreodont faunal "Zone C" of Brule Formation, 2 mi. N.W. of Cedar Pass, White River drainage, "upper part of Upper *Oreodon* beds," Jackson County, South Dakota; collected by Ralph Mefferd and Morris F. Skinner, 1939 Figures 4–6, 52

REFERRED FROM WHITE RIVER DRAINAGE, 1 MILE EAST OF NORBECK PASS, JACKSON COUNTY, SOUTH DAKOTA (COLLECTED BY MORRIS F. SKINNER AND ASSOCIATES, 1946)

SKULL		F:A.M.
Partial skull with P^1(br.)–M^3(br.)	(w‡)	72059

2. **Merycoidodon (Blickohyus) lynchi,**[1] new species

From "Zone D" of Brule Formation, Pennington County, South Dakota; referred remains from Jackson and Washabaugh counties, South Dakota; Sioux County, Nebraska; and Colorado

DESCRIPTION

SKULL: Approximate size of holotype of *M.* (*B.*) *galushai,* but more robust; smaller than examples of *M.* (*Anomerycoidodon*) *lambi* and *Paramerycoidodon* (*Barbourochoerus*) *major;* less robust than those of *P.* (*Gregoryochoerus*) *wanlessi* (all four of these species also occur in "Zone D" of the Brule); sagittal crest prominent; tendency for frontal to be convex; nasals narrow to moderately wide, posterior border acute to obtuse; orbit directed mostly upward and forward; lacrimal fossa smaller and shallower than in holotype of *M.* (*B.*) *galushai;* infraorbital foramen in area above P^3; auditory bulla inflated, long vertically, larger than in holotype of *M.* (*B.*) *galushai* and examples of *Otionohyus* (*Otarohyus*) *alexi,* and smaller than examples of *M.* (*A.*) *lambi, P.* (*B.*) *major,* and *P.* (*G.*) *wanlessi.*

MANDIBLE: Deeper than holotype of *M.* (*B.*) *galushai,* shallower than examples of *P.* (*B.*) *major.*

DENTITION: More robust than in holotype of *P.* (*B.*) *galushai,* especially premolars; P^1–P^3 each with weak anterior intermediate crest [less prominent than in examples of *P.* (*B.*) *galushai*]; molars usually robust, similar to examples of *P.* (*B.*) *major.*

LIMBS: Moderately heavy; within size range of *Merycoidodon culbertsonii,* shorter than examples of *P.* (*B.*) *major* and *P.* (*G.*) *wanlessi.* (See proportions, chart 3.)

MEASUREMENTS: Tables 2 and 7 (pp. 74 and 146).

ILLUSTRATIONS: Figures 4–6, 19–23, 52.

DISCUSSION

Remains of *Merycoidodon* (*Blickohyus*) *lynchi* from "Zone D" of the Brule are well represented in the collections in contrast to the scarcity of examples of *M.* (*B.*) *galushai,* the ancestral species, from "Zone C." The two faunal zones "A" and "D" of the Brule have yielded a much larger amount of oreodont material than have zones "B" and "C."

The dentitions of examples of *M.* (*B.*) *lynchi* are intermediate in size between those of *M.* (*A.*) *lambi* (with lighter dentition) and those of *P.* (*B.*) *major* (with more robust

[1] Named in honor of the late John Lynch, who for many years was chief field assistant to Charles H. Falkenbach for the Frick Laboratory.

dentitions). The posteriorly shortened skulls of *M.* (*B.*) *lynchi* are distinctive when compared with examples of the two other mentioned species.

The F:A.M. specimens were collected by Morris Skinner and associates; and the U.N.S.M. examples, by Bertrand Schultz and associates.

Twenty-eight specimens are here recorded:

HOLOTYPE

Skull with C/–M^3 and partial right ramus with I_2–M_1. (M+)	F:A.M. 45297	From oreodont faunal "Zone D" of Brule Formation, SW. side of Sheep Mt., Cheyenne River drainage, Pennington County, South Dakota; collected by Gordon Fletcher, Ralph Mefferd, and Morris F. Skinner, 1938 Figures 4–6, 52

REFERRED FROM (A) GENERAL AREA, SOUTH DAKOTA, (B) SHANNON, (C) JACKSON, AND (D) WASHABAUGH COUNTIES, SOUTH DAKOTA; (E) SIOUX COUNTY, NEBRASKA, AND (F) COLORADO

A. FROM SOUTH DAKOTA

FROM "CHEYENNE RIVER," 1894:

SKULL AND MANDIBLE

Skull with I^1–M^3 (P^1, and M^1–M^2 br.) and fragments of mandible with I_1–I_3 and M_3	(w‡+)	A.M. 1288

FROM QUESTIONABLE LOCALITY, 1892:

2 SKULLS

Partial skull with I^1–I^3 alv. and C/(br.)–M^3 (P^1–M^1 alv. and M^2–M^3 br.)	(w‡‡)	614
Partial skull with I^1–C/ rt. and P^1(br.)–M^3	(w)	619

B. FROM CHEYENNE RIVER BASIN, SHANNON COUNTY, SOUTH DAKOTA

FROM HIGH DIVIDE[1] IN VICINITY OF HEAD OF E. FORK OF BIG CORRAL DRAW:

2 SKULLS AND MANDIBLES

Partial skull with I^1–I^2 br. and I^3–M^3 (C/ br.) and mandible (attached) with I_1–M_3	(w‡)	F:A.M. 45282
Partial skull with I^3–M^3 and mandible with I_2–/C rt. and P_1(br.)–M_3 . . . . . . Above M^3 with small AP measurement.	(w+)	45322

SKULL

Partial skull with P^1(br.)–M^3	(w+)	45324

FROM AREA NEAR HEAD OF W. FORK OF BIG CORRAL DRAW:

2 SKULLS AND MANDIBLES (ATTACHED)

Skull with C/ and P^1–M^3 br. and mandible with P_1–M_3 br.	(w‡+)	72090
Partial skull with C/(br.)–M^3 and mandible with /C(rt.)–M_3 (P_1–P_2 br.)	(w)	45285

FROM HEAD OF BIG CORRAL DRAW:

SKULL

Skull with C/–P^2 rt. and P^3–M^3	(w+)	45289

B′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM HEAD OF WIND CREEK, E. SIDE OF SHEEP MT.:

[1] In divide area between the Cheyenne River and White River drainages.

	SKULL AND MANDIBLE		F:A.M.
Anterior portion of skull with $C/–M^3$ and mandible with $/C$(br.)–M_3		(W)	45286

SKULL AND MANDIBULAR RAMUS

Right side of skull with P^2–M^3 (P^4 br.) and right ramus with P_1–P_4 br. and M_1–M_3 . . . . (M+) 72086

FROM HEAD OF SPRING CREEK:

2 SKULLS AND MANDIBLES (ATTACHED)

Skull with I^1(alv.)–M^3 ($C/$ br.) and mandible with I_1–$/C$ rt. and P_1(br.)–M_3 . . . (W+) 72083

Skull with $C/–M^3$ and mandible with P_1–M_3 . . . . (W+) 72085

SKULL

Skull with I^3–M^3 . . . . (W) 72087

FROM S. AND E. OF COTTONWOOD PASS:

MAXILLAE AND MANDIBLE

Left and right maxillae with P^2–M^3 and partial mandible with P_1(br.)–M_3 . . . . (M+) 72091

SKULL

Partial skull with $C/–P^1$ rt. and P^2(br.)–M^3 . . . . (W‡) 45290

Above M^3 with small anteroposterior measurement.

C. FROM WHITE RIVER DRAINAGE, JACKSON COUNTY, SOUTH DAKOTA

FROM $\frac{1}{4}$ MI. W. OF CEDAR PASS:

SKULL — F:A.M.

Skull with $C/$(rt.)–M^3 . . . . (M+) 72101

FROM $3\frac{1}{2}$–4 MI. NW. OF INTERIOR:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^3–$C/$ br. and P^1–M^3, mandible with I_3(rt.)–M_3, 2 scapulae (1 partial), 2 humeri (1 partial), 2 partial radii, 2 ulnae, 2 femora, 2 tibiae, 2 astragali, 2 calcanea, partial pes, pelvis, and vertebrae. Figures 19–23 (in part) . . . . . (–M) 72114

The field record associated with the above specimen indicates "Upper *Oreodon* or Lower *Leptauchenia*" for the faunal zone. It is here considered that the specimen must have been collected from the "Lower *Leptauchenia*" zone (=lower part of "Zone D" of the Brule).

D. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM E. BRANCH OF REDWATER CREEK:

2 SKULLS AND MANDIBLES (ATTACHED) — F:A.M.

Partial skull with $C/$(rt.)–M^3 and partial mandible with I_2–$/C$ alv. and P_1–M_3 . . (W+) 72103

Partial skull with P^1–M^3 and partial mandible with P_3–M_3 . . . . (W‡) 72104

FROM E. SIDE OF POTATO CREEK:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^3–M^3 and partial mandible with P_1–M_3 . . . . (W) 72106

FROM 8–9 MI. S. AND 2 MI. W. OF INTERIOR:

SKULL AND MANDIBLE (ATTACHED)

Anterior portion of skull with P^3–M^3 and partial mandible with P_1(rt.)–M_3(br.) . . (W+) 72110

FROM HAY CREEK AREA:

TABLE 3

Paramerycoidodon, New Genus, *Paramerycoidodon* (*Barbourochoerus*), New Subgenus, and *Paramerycoidodon* (*Gregoryochoerus*), New Subgenus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*P. georgei*, new species	*P.* (*B.*) *harrisi*, new species	*P.* (*B.*) *bacai*, new species	*P.* (*B.*) *major* (Leidy)		*P.* (*G.*) *wanlessi*, new species	*P.* (*G.*) *meagherensis* (Koerner)
	Holotype F:A.M. 45143	Holotype F:A.M. 45264	Holotype U.N.S.M. 28191	Holotype U.S.N.M. 19099	Referred F:A.M. 45298	Holotype F:A.M. 72014	Holotype Y.P.M. 13948
Stage of wear of teeth	(M+)	(w‡)	(w‡)	(w+)	(w‡)	(w+)	(w)
Length (incl. supraoccipital crest and incisors)	((210))	—	((225))	—	255.5	216	238.5
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	((190))	—	((197))	—	222	190	207
Width (max.)	—	—	—	—	158	131	127
Width of brain case (max.)	58.5	—	54.5	—	65	64	63
Width, interorbital (min.)	59.5	(60)	55.5	—	67.5	57	62.5
Distance from anterior rim of orbit to anterior base of C/	((88))	—	(80)	—	98	77	94.5
Distance from anterior rim of orbit to supraoccipital crest	(133)	—	(137)	—	164	141.5	150
Length of nasals	((90))	((94))	—	—	((100))	(73)	(100)
Width of muzzle at infraorbital foramina	58	62	62.5	—	61	55.5	58.5
Width across canines	—	—	—	—	(60)	49	42
Length, C/–M^3 incl.	((108))	—	(106)	—	121.5	105	115.5
Length, P^1–M^3 incl.	94.5	94.5	(97)	—	100.5	90	99.5
Length, P^1–P^4 incl.	47.5	44.5	(42)	—	48.5	43.5	48
Length, M^1–M^3 incl.	51.5	52.5	56.5	58	53	50	52.5
Width of M^3 (max.)	21	21	25	22	23	20.5	19.5
Depth of malar below orbit	17.5	18	18	—	22.5	18.5	15.5

TABLE 3—(*Continued*)

MANDIBULAR RAMUS	*P. georgei*, new species	*P.* (*B.*) *harrisi*, new species	*P.* (*B.*) *bacai*, new species	*P.* (*B.*) *major* (Leidy)		*P.* (*G.*) *wanlessi*, new species	*P.* (*G.*) *meagherensis* (Koerner)
	Referred F:A.M. 72210	Holotype F:A.M. 45264	Holotype U.N.S.M. 28191	Holotype U.S.N.M. 19099	Referred F:A.M. 45298	Holotype F:A.M. 72014	Holotype Y.P.M. 13948
Stage of wear of teeth	(w‡)	—	—	—	—	—	—
Length (max., incl. incisors)	((188))	—	—	—	201.5	(163)	189
Length, /C–condyle incl.	173.5	—	—	—	176	152	173
Depth of jaw under coronoid	((80))	—	—	—	100	89.5	92.5
Depth of jaw below anterior edge of M_3	38.5	—	—	—	50	40	42
Length, /C–M_3 incl.	116.5	—	—	—	122	103.5	114.5
Length, P_1–M_3 incl.	106	—	—	—	108	100	106
Length, P_1–P_4 incl.	50.5	—	—	—	49.5	46.5	49
Length, M_1–M_3 incl.	55.5	—	—	—	58.5	55	56.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

SKULL AND MANDIBLE		F:A.M.
Partial skull with C/(rt.)–M^3 and mandible with P_1–P_2 rt. and P_3–M_3	(w‡)	45292
SKULL, IMMATURE		
Anterior left side of skull with C/(br.)–dP^2–M^3(erupt.).	(I)	72141

E. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, U.N.S.M. COLL. LOC. SX-12, SIOUX COUNTY, NEBRASKA

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Anterior portion of skull with C/–M^3 and mandible with I_1–M_3	(w+)	28333

E′. FROM WHITE RIVER DRAINAGE, ROUND TOP AREA, U.N.S.M. COLL. LOC. SX-22, SIOUX COUNTY, NEBRASKA

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with I^1–M^3 (P^1–M^1 br.) and mandible with /C–M_3	(w‡+)	28067

F. FROM COLORADO (COLLECTED BY E. DEVANDORF, 1873)

SKULL		Y.P.M.
Partial skull with C/–P^2 br. and P^3–M^3	(w‡)	12609

Designated by Thorpe, 1937, as plesiotype of this species.

II. **PARAMERYCOIDODON**, NEW GENUS

GENOTYPE: *Paramerycoidodon georgei*, new species.

DESCRIPTION

SKULL: Small to medium in size; more robust than examples of *Merycoidodon;* basal lengths ranging from 183 to 207 mm., widths from 115 to 126 mm.; dolichocephalic; supraoccipital region narrow; supraoccipital wings moderately spread, extending posteriorly for short distance posterior to condyles; exoccipital foramen small; sagittal crest moderately high; brain case moderately inflated, more so than in examples of *Merycoidodon;* frontals flat, more so than average examples of *Merycoidodon;* nasals narrow to moderately broad, posterior border usually acute; nasal-maxilla anterior contact in area above posterior border of C/; orbit roundish to oblong (longest diameter is vertical) and directed outward, upward, and forward (with more slope externally from superior to inferior border than in examples of *Merycoidodon*); malar shallow, inferior border with sharp upward curve posteriorly; zygomatic arch more robust than in examples of *Merycoidodon,* slightly less so than in those of *P.* (*Barbourochoerus*); infraorbital foramen above P^3; lacrimal fossa moderately deep and roundish; premaxillae touching but not fused; muzzle more inflated than in examples of *Merycoidodon;* occipital condyle moderately light to moderately heavy; paroccipital process moderately light, anterior-external surface excavated; bulla small (minute), similar to bullae of *Merycoidodon;* postglenoid process robust, wider transversely than anteroposteriorly, long (vertically), external border with marked downward and inward slope.

MANDIBLE: Moderately robust (lighter in examples of *Merycoidodon*); postsymphysis below posterior portion of P_3; ramus moderately deep; inferior border of ramus almost straight to point posterior to M_3, then having a marked downward curve [curve less prominent in examples of *M.* (*Barbourochoerus*) and *P.* (*Gregoryochoerus*)]; occipital condyle large, wide transversely, more robust than examples of *Merycoidodon.*

DENTITION: Robust, more so than examples of *Merycoidodon;* tendency for exceptionally large premolars; external styles of superior molars very prominent; I^{1-3}_{1-3} larger than in *Merycoidodon;* P^1–P^3 each with prominent anterior intermediate crest, larger than in examples of *Merycoidodon* and *M.* (*Anomerycoidodon*); P^4 usually with short but prominent anterior intermediate crest.

LIMBS: Robust, more robust and tendency to be longer than examples of *Merycoidodon* and *M.* (*Anomerycoidodon*).

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6–9, 52 (skulls, mandibles, and dentitions), 19–23 (limbs).

DISCUSSION

The new genus *Paramerycoidodon* is confined to "Zone A" of the Brule. There seem to be close affinities between *Merycoidodon* and *Paramerycoidodon*. Perhaps both genera had an ancestor in common during early Chadron times. Both forms possess small (minute) bullae, but the skulls and dentitions of *Paramerycoidodon* are more robust than those of *Merycoidodon*.

Examples of *Paramerycoidodon* are here considered as ancestral to those of *P.* (*Barbourochoerus*) from zones "B," "C," and "D" of the Brule.

DISTRIBUTION

One species of *Paramerycoidodon* is known from the middle Oligocene (oreodont faunal "Zone A" of the Brule Formation) of South Dakota, Nebraska, Wyoming, and North Dakota. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

One species of *Paramerycoidodon* from five Oligocene localities is here recorded:

1. *Paramerycoidodon georgei,* new species, from Shannon County, South Dakota; referred remains from Pennington County, South Dakota; Sioux County, Nebraska; Niobrara County, Wyoming; and Stark County, North Dakota. ("Zone A" of Brule.)

HOLOTYPE: Partial skull, F:A.M. 45143. Figures 7–9, 52.

DETAILED LIST OF TYPE AND REFERRED SPECIMENS

PARAMERYCOIDODON

TOTAL AVAILABLE SPECIMENS: 38[1]

1. Paramerycoidodon georgei,[2] new species

From oreodont faunal "Zone A" of Brule Formation, Shannon County, South Dakota; referred remains from Shannon and Pennington counties, South Dakota; Sioux County, Nebraska; Niobrara County, Wyoming; and Stark County, North Dakota

DESCRIPTION

SKULL: Differs from examples of *Merycoidodon culbertsonii* (from same faunal zone) in the following characters: more brachycephalic; orbits somewhat larger and directed more upward; postglenoid process more massive. (See generic description.)

MANDIBLE: (See generic description).

DENTITION: (See generic description).

LIMBS: (See generic description).

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6–9, 19–23, 52.

DISCUSSION

Examples of *Paramerycoidodon georgei* exhibit the largest and most robust premolars of this subfamily. The basal lengths of the skulls are similar to those of examples of *Merycoidodon culbertsonii.* The skulls are similar to those of the previously mentioned species, but more massive.

The F:A.M. specimens from North Dakota and South Dakota were collected by Morris F. Skinner and associates, 1938–1940, 1944, 1950; the F:A.M. material from Wyoming, by Charles H. Falkenbach and associates, 1938, 1943; and the U.N.S.M. examples, by C. Bertrand Schultz and associates.

Thirty-eight specimens are here recorded:

HOLOTYPE

Partial skull with C/–P¹ rt. and P²–M³. (M+)	F:A.M. 45143	From oreodont faunal "Zone A" of Brule Formation, base of the lower nodules, 1½ mi. S. of Cottonwood Pass,[3] Cheyenne River drainage, Shannon County, South Dakota; collected by Gordon Fletcher, Ralph Mefferd, and Morris F. Skinner, 1938 Figures 7–9, 52

[1] Includes 35 F:A.M. and 2 U.N.S.M. specimens.

[2] Named after George Krochak, Registrar for the Frick Laboratory.

[3] The Cottonwood Pass area is in the divide region between the Cheyenne and White River drainages.

REFERRED FROM (A) SHANNON AND (B) PENNINGTON COUNTIES, SOUTH DAKOTA; (C) SIOUX COUNTY, NEBRASKA; (D) NIOBRARA COUNTY, WYOMING; AND (E) STARK COUNTY, NORTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM W. SIDE OF SHEEP MT.:

SKULL AND MANDIBLE (ATTACHED) F:A.M.

Skull with I^1(alv.)–M^3 and mandible with I_1–I_2 rt. and I_3–M_3 (/C br.) . . . . . (w‡⁺) 45230

FROM 2 MI. W. OF SHEEP MT.:

SKULL AND MANDIBULAR RAMUS

Partial skull with I^1–I^2 rt. and I^3–M^3 and partial right ramus with /C–P_4 . . . . (M) 45238

FROM 2½ MI. W. OF SHEEP MT. ON INDIAN CREEK:

2 SKULLS

Partial skull with I^1–M^3 . . . . (w+) 45239
Partial skull with P^2(rt.)–M^3 . . . . (M) 45246

FROM 1 MI. N. OF COTTONWOOD PASS[1]:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–M^3 and mandible with I_1–M_3 . . . . (w‡) 45245

FROM 1–1½ MI. S. OF COTTONWOOD PASS:

2 SKULLS

Partial skull with C/(rt.)–M^3 . . . . (w‡) 45112
Skull with I^1–M^3 . . . . (w) 45150

FROM BIG CORRAL DRAW:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Right side of skull with C/(rt.)–M^3, partial mandible with I_1–M_3, 2 partial scapulae, partial humerus, radius, 2 ulnae, 2 partial femora, partial tibia, 2 partial calcanea, 2 astragali, partial pelvis, vertebrae, and fragments. Figures 19–23 (in part) . . (w+) 72209
Included with the above specimen is a partial astragalus that is smaller than astragali associated with the above skeleton.

FROM HEAD OF LITTLE CORRAL DRAW:

SKULL AND MANDIBLE

Partial skull with I^1–M^3 and mandible with I_1–M_3. Figure 6 (in part) . . . . . . (w‡) 72210

FROM HEAD OF QUINN DRAW:

MANDIBLE AND METATARSAL

Partial mandible with I_1–M_3 (P_1 br.) and metatarsal III. Figure 23 (in part) . . . (w‡) 72211

FROM BATTLE CREEK DRAW:

SKULL

Partial skull with C/(rt.)–M^3 (P^1 br.) . . . . (w‡⁺) 49772

B. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM MILLER BASIN, CAIN CREEK:

3 SKULLS AND MANDIBLES

Partial skull with I^1–I^3 rt. and C/(br.)–M^3 and partial mandible (attached) with M_2(br.)–M_3 . . . . (w‡) F:A.M. 45161

[1] The two Cottonwood Pass localities are in the Big Corral Draw area in the divide region between the Cheyenne River and White River drainages.

F:A.M.

Skull with I^1–M^3 and mandible (attached) with I_1–M_3 . . . . (M) 45206

Partial skull with I^1–C/ rt. and P^1–M^3 and partial mandible with P_2–P_3 rt. and P_4–M_3(br.) . . . . (W+) 45209

SKULL

Partial skull with I^1–C/ rt. and P^1–M^3 . . . . (M+) 45221

MANDIBLE

Partial mandible with I_1–M_3 . . . . (W+) 72172

FROM E. SIDE OF MILLER BASIN:

SKULL AND MANDIBLE

Partial skull with I^1–C/ br. and P^1–M^3 and mandible (attached) with I_1–P_1 br. and P_2–M_3 . . . . (W‡) 45198

2 SKULLS

Skull with I^1–C/ rt. and P^1–M^3 . . . . (W‡$^+$) 45204

Partial skull with P^3(br.)–M^3 . . . . (W) 45205

FROM BASIN E. OF MILLER BASIN:

SKULL AND MANDIBLE

Partial skull with C/(rt.)–M^3 and mandible (attached) with /C–P_1 br. and P_2–M_3 . . . . (W‡$^+$) 45216

FROM 6–7 MI. W. OF CONATA:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with P^1(rt.)–M^3 and partial mandible with I_1–/C rt. and P_1–M_3 . . . (W) 72212

SKULL

Partial skull with I^1–C/ rt. and P^1–M^3 . . . . (M) 45164

FROM 4 MI. S. AND E. OF SCENIC:

2 SKULLS AND MANDIBLES

Partial skull with I^1–P^4 rt. and M^1–M^3 and mandible (attached) with I_1–P_1 br. and P_2(rt.)–M_3 . . . . (W‡$^+$) 45156

Partial skull with C/(rt.)–M^3 and partial mandible with P_1–P_2 rt. and P_3–M_3. Figures 6, 9 (in part) . . . . (W+) 45157

The dental series are illustrated to show comparison of the lightest premolar examples.

FROM N. OF SCENIC (A.M. EXPEDITION, 1941):

SKULL AND MANDIBLE A.M.

Partial skull with I^1(rt.)–M^3 and mandible with I_1(br.)–M_3 (I_2–I_3 alv.) . . . . . (W+) 39459

FROM 1 MI. E. OF IMLAY:

SKULL, MANDIBLE, AND RADIUS F:A.M.

Partial skull with I^1–P^1 rt. and P^2–M^3, partial mandible with I_1–P_1 rt. and P_2–M_3, and partial radius . . . . (W) 72207A

MANDIBULAR RAMUS, IMMATURE

Partial ramus with dP_2–M_3(germ, br.) . . . . (I) 72207B

The above two specimens were found associated in the field.

C. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM 1 MI. N. OF ALBERT MENG RANCH HOUSE (U.N.S.M. COLL. LOC. SX–14):

	SKULL	F:A.M.
Skull with I^3(br.)–M^3 (P^1 br.)	(w‡+)	72215

C′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–40:

	SKULL, MANDIBLE, AND ATLAS	
Partial skull with C/–P^1 rt. and P^2(br.)–M^3 (P^3–M^1 br.), partial mandible with P_1–M_3 br., and atlas	(w)	U.N.S.M. 28328

D. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SPRING DRAW AREA:

	SKULL AND MANDIBLE	F:A.M.
Partial skull with I^1–M^3 and mandible with I_1–M_3 (P_1 br.)	(w)	45128

FROM AREA E. OF U. S. HIGHWAY NO. 85:

	SKULL	
Partial skull with P^1–P^2 br. and P^3–M^3 (dP^4 on left side)	(–M)	45134

FROM SE. OF SPRING DRAW (KLEMKE PLACE):

	SKULL	
Partial skull with I^1–M^3	(w+)	72214

E. FROM 7 MILES SOUTH OF SOUTH HEART, STARK COUNTY, NORTH DAKOTA

	SKULL, MANDIBLE, AND ATLAS	F:A.M.
Partial skull with I^1–M^3, partial mandible with I_1–M_3, and atlas	(w‡+)	72213

IIA. PARAMERYCOIDODON (BARBOUROCHOERUS), NEW SUBGENUS

SUBGENOTYPE: *Paramerycoidodon (Barbourochoerus) bacai,* new species.

DESCRIPTION

SKULL: Small to medium size (includes largest skulls of subfamily); basal lengths ranging from 197 to 234 mm., widths from 115 to 180 mm.; dolichocephalic to mesocephalic; characters similar to those of *Paramerycoidodon* except for sagittal crest more prominent, supraoccipital wings extending more posteriorly, lacrimal fossa smaller (but as deep), malar deeper below orbit, and larger bulla (well inflated).

MANDIBLE: Characters similar to those of *Paramerycoidodon* except for the following: muzzle more expanded, ramus slightly more robust, ramus deepening more rapidly posteriorly.

DENTITION: Characters similar to those of *Paramerycoidodon* but with larger series in later deposits in the geologic sequence; P^1–P^3 with weak to moderately strong anterior intermediate crests.

LIMBS: Robust (similar to examples of *Paramerycoidodon*).

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6–9, 52 (skulls, mandibles, and dentitions), 19–23 (limbs).

DISCUSSION

Examples of *Paramerycoidodon (Barbourochoerus)* are rare in oreodont faunal zones "B" and "C" of the Brule, but relatively common in "Zone D." This same distribution of oreodont remains, however, is noted in most of the phyla of oreodonts, i.e., zones "B" and "C" have not produced so many specimens as zones "A" and "D."

Paramerycoidodon (Barbourochoerus) apparently was derived directly from *Paramerycoidodon.* The skulls of the subgenus differ from those of the genus in having inflated bullae, and from those of *Merycoidodon (Anomerycoidodon)* by possessing more robust dentitions.

This subgenus includes the largest species [*P.* (*B.*) *major*] of the subfamily Merycoidodontinae. The skulls are as long as but wider than examples of *Subdesmatochoerus shannonensis,* a species included in the Desmatochoerinae.

The proposed sequence of the species of *Paramerycoidodon* (*Barbourochoerus*) is as follows: *M.* (*B.*) *bacai* from "Zone B" of the Brule, and *M.* (*B.*) *major* from "Zone D" of the Brule. (Examples from "Zone C" are not available.)

Distribution

Two species of *Paramerycoidodon* (*Barbourochoerus*) are known from the upper Oligocene (oreodont faunal zones "B" and "D" of the Brule) of Nebraska and South Dakota. (See geologic distribution chart, p. 22.)

Summary of Species and Types

Two species of *Paramerycoidodon* (*Barbourochoerus*) from five Brule localities are here recorded:

1. *Paramerycoidodon* (*Barbourochoerus*) *bacai,* new species, Sioux County, Nebraska; referred from Sioux County, Nebraska, and Shannon County, South Dakota. (Oreodont faunal "Zone B" of Brule.)

HOLOTYPE: Skull, U.N.S.M. 28191. Figures 7–9, 52.

2. *Paramerycoidodon* (*Barbourochoerus*) *major* (Leidy), from South Dakota; referred remains from Washabaugh, Pennington, Shannon, and Jackson counties, South Dakota; and Sioux County, Nebraska. ("Zone D" of Brule.)

HOLOTYPE: Partial right maxilla, U.S.N.M. 19099. Figure 9.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS

PARAMERYCOIDODON (BARBOUROCHOERUS)

TOTAL AVAILABLE SPECIMENS: 58[1]

1. Paramerycoidodon (Barbourochoerus) bacai,[2] new species

From oreodont faunal "Zone B" of the Brule Formation, Sioux County, Nebraska; referred remains from Sioux County, Nebraska; and Shannon County, South Dakota

Description

SKULL: Within size range of examples of *Paramerycoidodon georgei* (from "Zone A" of the Brule), smaller than those of *P.* (*B*) *major* (from "Zone D"); brain case intermediate in width between examples of *P. georgei* and those of *P.* (*B.*) *major*; greater postorbital constriction than in the latter species; auditory bulla inflated, marked hyoidal groove and pit, decidedly larger than small (minute) bulla of *P. georgei,* but smaller than bullae of *P.* (*B.*) *major.*

MANDIBLE: (Unknown).

[1] Includes 46 F:A.M. and 2 U.N.S.M. specimens.

[2] Named in honor of Alfred Baca from Lusk, Wyoming, who has aided the Frick Laboratory field parties at numerous times with his knowledge of the geography and history of eastern Wyoming and northwestern Nebraska.

DENTITION: Equal in size to larger examples of *P. georgei,* and shorter than examples of *P.* (*B.*) *major*; P^1–P^3 each with moderately strong anterior intermediate crest.

LIMBS: (Unknown).

MEASUREMENTS: Table 3 (p. 84).

ILLUSTRATIONS: Figures 7–9, 52.

Discussion

The dentition of the holotype of *P.* (*B.*) *bacai* is badly fractured, and the cracks are filled with matrix. The individual teeth, however, are enormous. With allowances made for the cracks, the teeth would still be at least as robust as the largest examples of *P. georgei.* Figure 9 illustrates the dentition of the holotype and that of a lighter example, which has been referred to this species. Noteworthy is the M^3 of the latter, as it has a greatly reduced last lobe.

This species presumably gave rise to *P.* (*B.*) *major* in "Zone D" of the Brule. Unfortunately no specimens representing this phylogenetic line are known from "Zone C." Specimens are needed from both zones "B" and "C" in order to better understand the actual relationship between *P.* (*B.*) *bacai* and *P.* (*B.*) *major.*

The U.N.S.M. specimens were found by C.

Bertrand Schultz and associates, 1933 and 1940; and the F:A.M. specimen was collected by Morris F. Skinner and associates, 1938.

Three specimens are here recorded:

HOLOTYPE

Partial skull with P^1(rt.)–M^3 (w‡)	U.N.S.M. 28191	From oreodont faunal "Zone B" of Brule Formation, White River drainage, U.N.S.M. Coll. Loc. SX–19, 11¼ mi. N. and 8½ mi. W. of Crawford, Sioux County, Nebraska; collected by C. Bertrand Schultz and associates (E. L. Blue, Frank W. Crabill, Frank R. Denton, Loren C. Eiseley, Robert Long, Marian Schultz, Mylan Stout, and Eugene Vanderpool, 1933) Figures 7–9, 52

REFERRED FROM (A) SIOUX COUNTY, NEBRASKA; AND (B) SHANNON COUNTY, SOUTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, U.N.S.M. SX–37, SIOUX COUNTY, NEBRASKA

SKULL		U.N.S.M.
Partial skull with C/–M^3. Figure 9	(w)	28469

B. FROM EAST SIDE OF HARNEY SPRINGS, WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

SKULL		F:A.M.
Partial skull C/(rt.)–M^3	(w‡)	45264

The M^3 exhibits a reduced last lobe. It is not pronounced, but is similar to that found in *Merycoidodon (Anomerycoidodon) lambi*, referred, F:A.M. 72124 (p. 174, fig. 5).

2. **Paramerycoidodon (Barbourochoerus) major** (Leidy)

From oreodont faunal "Zone D" of the Brule, South Dakota; referred remains from Washabaugh, Pennington, Shannon, and Jackson counties, South Dakota; and Sioux County, Nebraska

Oreodon major LEIDY, 1853, p. 392 (no description); 1854a, p. 55, pl. 4, fig. 6 ("syn. *Merycoidodon major*")[1]; 1869, p. 99, pl. 7, fig. 1, pl. 8. GIEBEL, 1883, pl. 44, fig. 11.

Oreodon major? LEIDY, 1854a, p. 113.

Oreodon (Eporeodon) major (Leidy): KAMPFEN, 1905, p. 592.

Eucrotaphus major (Leidy): COPE, 1884a, pp. 519, 520, *Eucrotaphus major major* (Leidy).

Eucrotaphus? major (Leidy): THORPE, 1924a, p. 123.

Eucrotaphus (Oreodon) major (Leidy): SCOTT AND OSBORN, 1887b, p. 155.

Eporeodon (=Eucrotaphus) major (Leidy): MATTHEW, 1909, p. 109.

Eporeodon (Eucrotaphus) major (Leidy): O'HARRA, 1910, p. 109, pl. 44.

Eporeodon (?Eucrotaphus) major (Leidy): COOK, 1912, p. 39. O'HARRA, 1920, p. 154, pl. 22.

Eporeodon major (Leidy): MARSH, 1875, p. 250; 1897, p. 524, fig. 98. OSBORN AND WORTMAN, 1894, p. 218, fig. 5d. NICHOLSON AND LYDEKKER, 1889, p. 1326, fig. 1201. THORPE, 1937, p. 74, fig. 7, pl. 6, figs. 1–3. SCOTT, 1940, p. 679, pl. 72, figs. 1–1a.

Eporeodon major major (Leidy): THORPE, 1924b, p. 223.

Eporeodon (?) major (Leidy): DOUGLASS, 1901b, p. 266.

Eporeodon? major (Leidy): HAY, 1902, p. 667.

Merycoidodon culbertsonii Leidy (in part): LEIDY, 1854b, p. 157 (*Oreodon major?* and *Merycoidodon major?* syn. of *Oreodon major*).

CHARACTERS

SKULL: Largest examples of the Merycoidodontinae; mesocephalic; supraoccipital wings produced posteriorly beyond occipital condyles (greater posterior projection in male[2] than in fe-

[1] It is not clear as to where the synonym was previously published; perhaps Leidy was emphasizing his preference of *Oreodon* to *Merycoidodon*.

[2] See p. 461 for discussion of sex characters.

male examples); sagittal crest high and robust (more robust in male examples), most robust of subfamily (sagittal crest approaching very prominent crests noted in *Desmatochoerus*); nasals long, extending posteriorly beyond anterior border of orbit, posterior border subacute; orbit oblong vertically, proportionately small for size of skull; zygomatic arch moderately robust to robust (more robust in male examples); lacrimal fossa moderately deep, somewhat shallower than in *P.* (*B.*) *bacai;* muzzle inflated (more so in male examples); occipital condyles larger than in *P.* (*B.*) *bacai;* bulla well inflated, oblong (anteroposteriorly) in outline [in contrast to rounded examples of *P.* (*G.*) *wanlessi* from same faunal zone]; postglenoid process robust and wide (laterally); posterior palate extending posteriorly for short distance beyond M^3.

MANDIBLE: Robust; postsymphysis in area below anterior portion of P_4; ramus increasing rapidly in depth posteriorly, inferior border with noticeable downward curve below and posterior to M_3; ascending ramus expanded, with condyle relatively low in comparison with condyles of other species in phylogenetic line.

DENTITION: Larger than examples at *P.* (*B.*) *bacai;* more robust than examples of *Merycoidodon* (*Anomerycoidodon*) *lambi* and those of *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi,* all from "Zone D" of the Brule; P^1–P^3 each with weak anterior intermediate crest; P_2–P_4 each with posterior intermediate crest (more prominent than superior anterior intermediate crests); C/ and P_1 robust; /C prominent.

LIMBS: Most robust of the subfamily; slightly longer than examples of *M. culbertsonii.*

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6–9, 19–23, 52.

DISCUSSION

The holotype of *Paramerycoidodon* (*Barbourochoerus*) *major* (Leidy) is a partial right maxilla, U.S.N.M. 19099, which have very few field data associated with it. Thorpe[1] did not locate the holotype, but reported it as a "... right maxillary with molar series, collected by Dr. Owen about 1853," and listed no number. He used an "Allotype, Cat. No. 10863 A.N.S.P., a remarkably well-preserved skull," as the basis for the characters of the species *"Eporeodon" major.* Leidy's original holotype, however, is in the United States National Museum and must be used as the basis for the specific description. The present writers agree with Thorpe that the "Allotype," A.N.S.P. 10863, should be referred to this species. The fact that the holotype is fragmentary and consists of only a maxilla with M^1–M^3 resulted in this species' being considered under several different genera and subgenera by various workers. Actually the remains of *P.* (*B.*) *major* are the most common fossils representing the Merycoidodontinae from "Zone D" of the Brule. However, remains of *Leptauchenia decora* are the most common of all oreodonts from "Zone D."

Thorpe[2] also referred a specimen to *P.* (*B.*) *major* from the John Day of Oregon, and stated: "A single specimen, Cat. No. 12400 Y.P.M., in the Marsh Collection, from Turtle Cove, John Day Valley, Oregon, is referred to *E.* [=*Eporeodon*] *major.* It is middle John Day in age and in general coincides fairly closely, though not exactly, with this Great Plains form." The present writers, however, have not seen any evidence of *P.* (*B.*) *major* from the middle or upper John Day deposits. The middle and upper John Day deposits appear to be approximately equal in age to the conclusion, of course, is based on the stage of Harrison Formation of the Great Plains.[3] This development of the oreodont fauna from the John Day deposits.

It appears to the writers that the material referred to *P.* (*B.*) *major* shows evidence of sex variation. The variation observed here is similar to that already noted in the published reports on the Ticholeptinae and the Promerycochoerinae. The wider and more massive skulls are considered to be the male examples. It should be noted that in the above two subfamilies evidence of sex variation becomes more apparent during the latter part of the geologic history of the various phylogenetic

[1] 1937, p. 74. Falkenbach later found the holotype in the collection of the United States National Museum.

[2] 1937, p. 75.

[3] Schultz and Falkenbach, 1949, p. 89, chart 3; this report, p. 397.

lines. This is also seen in examples of *P.* (*B.*) *major,* which is the latest known form in a phylogenetic line of the Merycoidodontinae. In the Ticholeptinae, this variation is best exemplified in the medial Pliocene species *Ustatochoerus major*[1] in which the lighter and narrower skulls are considered to be the females, and the more robust ones the males. The same variation was also noted in the early Miocene species *Promerycochoerus carrikeri.*[2]

In the present study it has become obvious that end species of a phylum, regardless of the geologic age, is noticeably different morphologically from the ancestral forms. In most phylogenetic lines, the forms from various geologic zones differ primarily in size. Size, therefore, can be considered the most important single character. However, there are other significant character changes as well. Usually the greatest size development took place late in the geologic history of a phylum. The last species in the phylum seems to have developed into two groups with similar characters, except that one assemblage possessed lighter and narrower skulls and the other more robust ones. These differences are here considered to be associated with sex variation. It is of interest to note that in *P.* (*B.*) *major,* also the last recognized member of a phylogenetic line, the same apparent differences are to be observed.

It is here considered that *Merycoidodon* and *Paramerycoidodon* had an ancestor in common during early Chadron times. Evidence points to the fact that, while the skull characters in both phylogenetic lines were evolving during Brule times, very little change was taking place in the actual lengths of the limb elements, but the limbs were becoming more robust. For example, the limbs of *Merycoidodon culbertsonii browni* from "Zone C" at the Chadron are approximately the same length as those of *M. culbertsonii* from "Zone A" of the Brule, but are lighter. The limbs of *M.* (*A.*) *lambi* from "Zone D" of the Brule are approximately the same length, but heavier, than those of *M. culbertsonii.* Examples of *P.* (*B.*) *major* are similar in length, but are even more robust.

Remains of *P.* (*B.*) *major* are used primarily for the basis of the subgeneric description, since examples of this species are the most plentiful and complete of the genus.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1938–1940, 1945, 1950; and the U.N.S.M. examples, by C. Bertrand Schultz and associates, 1934 and 1950.

Fifty-five specimens are here recorded:

HOLOTYPE

Partial right maxilla with M^1–M^3. (W+)	U.S.N.M. 19099	From oreodont faunal "Zone D"[3] of Brule Formation, South Dakota (Owen's collection) Figured by Leidy, 1854a, pl. 4, fig. 6 Figure 9

REFERRED FROM (A) GENERAL AREA, SOUTH DAKOTA: (B) WASHABAUGH, (C) PENNINGTON, (D) SHANNON, AND (E) JACKSON COUNTIES, SOUTH DAKOTA; AND (F) SIOUX COUNTY, NEBRASKA

A. FROM GENERAL AREA,[4] SOUTH DAKOTA

SKULL		A.N.S.P.
Skull with I^1–M^3	(M+)	10863

Collected by F. V. Hayden "from the Mauvaises Terres of White River, Dakota." Figured by Leidy, 1869, pl. 7, fig. 1, pl. 8; Giebel, 1883, pl. 44, fig.11 (in part); Nicholson and Lydekker, 1889, fig. 1201 (in part); O'Harra, 1910, pl. 44; 1920, pl. 22; Marsh, 1897, fig. 98; Thorpe, 1937, pl. 6, figs. 1–3.

Designated as allotype by Thorpe, 1937.

[1] Schultz and Falkenbach, 1941, p. 11, fig. 6.
[2] Schultz and Falkenbach, 1949, p. 94.
[3] The present writers assume that the holotype is from "Zone D" of the Brule Formation, since the referable material, which has associated geologic data, is from "Zone D."
[4] Exact geographic localities unknown.

SKULL, MALE EXAMPLE		A.M.
Partial skull with I^1–P^1 rt. and P^2–M^3	(w‡⁺)	612
Collected in 1892.		
SKULL, FEMALE EXAMPLE		
Partial skull with C/–P^1 rt. and P^2–P^4 erupt. and M^1–M^3. Figure 52	(–M)	1038

Above specimen collected in 1892, and figured by Osborn and Wortman, 1894, fig. 5d; Thorpe, 1937, fig. 7.

The postglenoid processes of the above skull are more like examples of *M.* (*A.*) *lambi;* the teeth, however, are more massive than in that species.

SKULL AND MANDIBLE (ATTACHED)		Y.P.M.
Partial skull with I^1–M^3 and mandible with P_1–M_3	(w‡)	12273

Tentatively referred to this species by Thorpe, 1924b. Collected by H. F. Wells, 1894, and "shipped from Hermosa," South Dakota.

B. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

From Hay Creek Area:

Male Examples

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS		F:A.M.
Skull with I^1–I^2 rt. and I^3–M^3 (C/–P^1 br.), mandible with I_1–M_3, 2 humeri, 2 radii, ulna, partial manus, 2 femora, 2 partial tibiae, astragalus, calcaneum, pelvis, and vertebrae. Figures 6–9, 19–23	(w‡)	45298
Partial skull with C/–M^3(br.), mandible (attached) with I_1–P_2 br. and P_3–M_3, and partial manus	(w‡⁺)	45311
5 SKULLS AND MANDIBLES (ATTACHED)		
Partial skull with I^1–C/ rt. and P^1–M^3 and mandible with I_1–/C rt. and P_1–M_3	(w+)	45306
Skull with I^1–M^3 and mandible with I_1–M_3	(w‡)	45307
Anterior portion of skull with I^1–I^3 rt. and C/(br.)–M^3 and mandible with I_1–/C rt. and P_1(br.)–M_3	(M+)	45308
Skull with I^1(rt.)–M^3 and mandible with I_1–M_3	(M+)	45310
Anterior portion of skull with C/(br.)–M^3 and mandible with I_1–M_3 (I_3 rt.)	(w‡)	45312
2 SKULLS		
Skull with C/–P^3 br. and P^4–M^3	(w‡⁺)	45315
Anterior portion of skull with I^1–I^3 rt. and C/(br.)–dP^1–M^2	(I)	72115

Female Examples

4 SKULLS AND MANDIBLES		
Skull with I^1–M^3 (I^2 alv.) and mandible (attached) with I_1–I_3 rt. and /C(br.)–M_3	(w‡⁺)	45303
Skull with I^1–M^3 (C/–P^1 br.) and mandible (attached) with I_1–P_1 br. and P_2–M_3	(w‡⁺)	45304
Partial skull with C/–P^1 rt. and P^2–M^3 and mandible with I_1–M_3 (/C–P_1 br.)	(w)	45309
Partial skull with I^1–dP^2–M^3(erupt., br.) and mandible with I_1–dP_1–M_3(erupt.)	(I)	72116
2 SKULLS		
Skull with I^1–M^3 (P^1 br.)	(M+)	45313
Partial skull with I^1–P^1 rt. and P^2(br.)–M^3 (P^3 br.)	(w+)	45314

From E. Side of Potato Creek:

Male Examples

SKULL, MANDIBLE, AND PELVIS		
Skull with I^1–M^3, mandible (attached) with I_1–M_3, and partial pelvis	(w‡)	72117

4 SKULLS AND MANDIBLES (ATTACHED) F:A.M.

Partial skull with C/–P^1 br. and P^2–M^3 and mandible with P_1–P_2 br. and P_3–M_3	(w+)	45305
Skull with I^1–M^3 and mandible with I_1–M_3	(w+)	72118
Skull with I^2–C/ rt. and P^1–M^3 and mandible with P_1–M_3	(w‡)	72119

SKULL

Skull with C/–P^2 rt. and P^3–M^3	(w+)	72027

FROM CRAVEN BASIN, 6–7 MI. W. OF WAMBLEE:

MALE EXAMPLES

2 SKULLS AND MANDIBLES (ATTACHED)

Skull with I^2–M^3 and mandible with I_1(rt.)–M_3	(w‡+)	72121
Skull with I^1–M^3 and mandible with I_1–M_3	(w‡)	72122

SKULL

Skull with C/(br.)–M^3	(w‡)	72123

FROM 8–9 MI. S. AND 2 MI. W. OF INTERIOR:

SKULL

Partial skull with P^4–M^3	(w‡)	45316

C. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM NE. FACE OF SHEEP MT.:

SKULL AND MANDIBLE, MALE EXAMPLE F:A.M.

Partial skull with C/–P^2 rt. and P^3–M^3 and partial mandible with P_1–P_3 br. and P_4–M_3	(w+)	45326

C′. FROM CHEYENNE RIVER DRAINAGE, FIRST CANYON NORTH OF SCHOOL OF MINES CANYON, PENNINGTON COUNTY, SOUTH DAKOTA

MALE EXAMPLES

3 SKULLS AND MANDIBLES F:A.M.

Skull with I^1(br.)–M^3 and mandible with I_1–P_1 br. and P_2–M_3	(w)	72304
Skull with C/(br.)–M^3 and mandible with /C(rt.)–M_3	(w)	72305
Partial skull with P^2–M^3 and mandible (attached) with M_2(br.)–M_3	(w+)	72306

D. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM ¾–1¼ MI. S. OF COTTONWOOD PASS,[1] BIG CORRAL DRAW AREA:

MALE EXAMPLES

SKULL, MANDIBLE, AND SKELETAL ELEMENTS F:A.M.

Skull with I^2–M^3, mandible (attached) with I_1–M_3, partial ulna, and vertebrae	(w+)	72020

SKULL, MANDIBLE (ATTACHED), AND FEMUR

Skull with I^1–M^3, mandible with I_1–M_3, and partial femur	(w)	45317

SKULL AND MANDIBLE (ATTACHED)

Partial skull with C/–P^3 rt. and P^4–M^3 br. and fragmentary mandible	(w‡)	45318

FEMALE EXAMPLES

FROM HEAD OF E. FORK OF BIG CORRAL DRAW:

SKULL AND MANDIBLE (ATTACHED)

Skull with I^1–I^3 br. and C/–M^3 and mandible with I_1–/C br. and P_1–M_3	(w)	45319

[1] In the divide area between the Cheyenne River and White River drainages.

2 SKULLS AND MANDIBLES (ATTACHED) F:A.M.

Skull with I^1–M^3 and mandible with I_1–M_3 . . . . (w) 72019
Partial skull with C/ and P^1–M^3 rt. and fragments of mandible . . . . (w) 72125

SKULL

Partial skull with C/(rt.)–M^3 . . . . (w‡) 72307

FROM BETWEEN BIG CORRAL DRAW A[illegible]WOOD CREEK:

[illegible]D MANDIBLE

Partial skull with I^1–M^3 and mandible with I_1–M_3. . . . . (M+) 45320

D′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM HEAD OF SPRING CREEK, SE. OF SHEEP MT.:

MALE EXAMPLES

2 SKULLS AND MANDIBLES (ATTACHED) F:A.M.

Partial skull with I^2–C/ br. and P^1–M^3 and mandible with P_1(br.)–M_3 . . . . . . (w) 72126
Skull with P^1(br.)–M^3 and mandible with I_1–P_1 br. and P_2–M_3 . . . . (w‡) 72127

FROM ½ MI. S. OF ROCK SPRINGS:

SKULL, IMMATURE

Partial skull with C/(rt.)–dP^2–M^3(germ) (dP^4 br.) . . . . (I) 72129

FROM 5 MI. NW. OF SHARP'S STORE:

MANDIBLE

Partial mandible with P_2–M_3(br.) . . . . (w‡⁺) 72235

E. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA, JACKSON COUNTY, SOUTH DAKOTA

FROM 1½–2½ MI. NE. OF CEDAR PASS:

SKULL AND MANDIBLE, MALE EXAMPLE

Partial skull with P^1–P^2 and P^4–M^3 and mandible (attached) with /C(br.)–M_3 (P_3 rt.) . . . . (w‡⁺) F:A.M. 72130

SKULL, FEMALE EXAMPLE

Anterior portion of skull with C/(br.)–M^3 . . . . (w‡⁺) 45302

FROM ¼–1 MI. E. OF CEDAR PASS:

SKULL AND MANDIBLE, MALE EXAMPLE

Partial skull with C/–M^3 and mandible with I_1–M_3 . . . . (w‡) 72216

SKULL, FEMALE EXAMPLE

Partial skull with C/(br.)–M^3. . . . . (w‡) 72131

FROM ¼–2 MI. W. OF CEDAR PASS:

SKULL AND SKELETAL ELEMENTS, MALE EXAMPLE

Partial skull with P^1(rt.)–M^3, partial scapula, partial humerus, partial radius, partial ulna, partial femora, partial tibia, astragalus, calcaneum, and fragments . . . . (w+) 72031

SKULL AND MANDIBLE (ATTACHED), FEMALE EXAMPLE

Anterior portion of skull with I^3(br.)–M^3 and partial mandible with /C–M_3. . . . (w+) 72096

FROM "400 YDS. E. OF ROAD," CEDAR PASS (COLLECTED BY JOHN CLARK, 1934):

SKULL AND MANDIBLE (ATTACHED)		P.U.
Skull with I^2–M^3 and mandible with I_1–M_3. Figured by Scott, 1940, pl. 72, figs. 1–1a	(w+)	14061

FROM CROW BUTTES, SOUTH DAKOTA:

SKULL		Y.P.M.
Skull	(w)	12447

Tentatively referred to *Eporeodon helenae* [=*O.* (*O.*) *h. helenae*, p. 131] by Thorpe, (1937, p. 70).

F. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–22:

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Skull with I^1–C/ br. and P^1–M^3 and mandible with I_1–M_3 (I_2–P_1 br.)	(w‡)	28341

FROM U.N.S.M. COLL. LOC. SX–26:

SKULL		
Left anterior portion of skull with P^1(rt.)–M^3(rt.)	(w+)	28139

IIB. PARAMERYCOIDODON (GREGORYOCHOERUS), NEW SUBGENUS

SUBGENOTYPE: *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi*, new species.

DESCRIPTION

SKULL: Small to medium in size; basal lengths ranging from 190 to 210 mm., widths from 120 to 145 mm.; mesocephalic; characters similar to those of *Paramerycoidodon* except supraoccipital wings more widely spread, sagittal crest higher and more prominent, brain case more inflated, malar slightly deeper below orbit, occipital condyles larger, bulla larger (inflated); characters similar to *P.* (*Barbourochoerus*) except for smaller size, sagittal crest less prominent, lacrimal fossa more restricted in size and depth, bulla more inflated.

MANDIBLE: Characters similar to those of *Paramerycoidodon* except for the following: ramus deeper posteriorly [similar in this respect to examples of *P.* (*Barbourochoerus*)], ascending ramus slightly shorter anteroposteriorly and deeper vertically; characters similar to those of *P.* (*Barbourochoerus*) except size smaller.

DENTITION: Characters similar to those of examples of *Paramerycoidodon;* similar to those of *P.* (*Barbourochoerus*) except somewhat smaller and lighter.

LIMBS: Lighter than examples of *Paramerycoidodon* and *P.* (*Barbourochoerus*), approximating those of *Merycoidodon.*

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6–9, 52 (skulls, mandibles, aand dentitions), 19 (limb).

DISCUSSION

Remains of *Paramerycoidodon* (*Gregoryochoerus*) are known only from the upper Oligocene and lower Miocene ("Zone D" of the Brule and Gering). Apparently *P.* (*G.*) *wanlessi* from "Zone D" gave rise to *P.* (*G.*) *meagherensis* from the Gering. This phylogenetic line is the only example in the oreodonts, except for several phyla of leptauchenids, in which the same genus is reported from both the Brule and the Gering. In the Desmatochoerinae, *Subdesmatochoerus* from the upper Brule gave rise to *Desmatochoerus* from the Gering, and, in the Promerycochoerinae, *Promesoreodon* from the upper Brule gave rise to *Mesoreodon* from the Gering. In the latter two cases the changes definitely appear to be of generic importance. In *P.* (*Barbourochoerus*), however, the change cannot be considered to be more than of specific importance. (See subfamily geologic distribution, Part 2, p. 416.)

It is here considered that the subgenus *P.* (*Gregoryochoerus*) evolved from either *Paramerycoidodon* or *P.* (*Barbourochoerus*).

The proposed sequence of species of *Paramerycoidodon* (*Barbourochoerus*) is as follows: *P.* (*B.*) *wanlessi* from "Zone D" of the Brule, and *P.* (*B.*) *meagherensis* from the

Gering Formation or deposits of equivalent age.

Distribution

Two species of *Paramerycoidodon* (*Barbourochoerus*) are known from the upper Oligocene (oreodont faunal "Zone D" of Brule) and the lower Miocene (upper Gering) of South Dakota, Nebraska, and Montana. (See geologic distribution chart, p. 22.)

Summary of Species and Types

Two species of *Paramerycoidodon* (*Gregoryochoerus*) from six Brule and Gering localities are here recorded:

1. *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi*, new species, from Shannon County, South Dakota; referred remains from Shannon, Pennington, Washabaugh, Jackson, and Fall River counties, South Dakota; and Sioux County, Nebraska. ("Zone D" of Brule.)

Holotype: Skull and mandible, F:A.M. 72014. Figures 6–9.

2. *Paramerycoidodon* (*Gregoryochoerus*) *meagherensis* (Koerner), from Meagher County, Montana; referred remains from Sioux County, Nebraska. (Gering or its equivalent.)

Holotype: Skull, mandible, and skeletal elements, Y.P.M. 13948.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PARAMERYCOIDODON (GREGORYOCHOERUS)

Total available specimens: 51[1]

1. Paramerycoidodon (Gregoryochoerus) wanlessi,[2] new species

From "Zone D" of the Brule Formation, Shannon County, South Dakota; referred remains from Shannon, Pennington, Washabaugh, Jackson, and Fall River counties, South Dakota; general area, South Dakota; and Sioux County, Nebraska

Description

Skull: Smaller than examples of *P.* (*Barbourochoerus*) *major*, larger than those of *Otionohyus* (*Otarohyus*) *alexi*, all from "Zone D" of the Brule; sagittal crest prominent but light, lighter than in examples of *P.* (*B.*) *major;* nasals may be acute or obtuse posteriorly; infraorbital foramen above P^3; lacrimal fossa restricted in size, smaller than in examples of *O.* (*O.*) *alexi;* bulla large and roundish, largest examples of the Merycoidodontinae, lacking a hyoidal groove; postglenoid process comparable with examples of *P.* (*B.*) *major,* more slope to external border than in those of *O.* (*O.*) *alexi.* (See subgeneric description.)

Mandible: Condyle smaller laterally than in examples of *P.* (*B.*) *major.* (See subgeneric characters.)

Dentition: Premolars crowded, P^1_1–P^3_3 usually set at slight angle to alveolar border; P^1–P^4 each with moderately prominent anterior intermediate crest, P_2–P_3 each usually with a weak posterior intermediate crest. (See subgeneric description.)

Limbs: Moderately light. (Known from partial humerus only.)

Measurements: Table 3 (p. 84).

Illustrations: Figures 6–9, 19, 52.

Discussion

Remains of *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi* seem to represent a smaller and lighter-skulled form than *P.* (*Barbourochoerus*) *major,* which also is reported from "Zone D" of the Brule. *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi* differs from *P.* (*B.*) *major* in the following characters: smaller size of the skull, lighter sagittal crest, more rounded bulla, and smaller dental series.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1938-1941, 1945, 1950, 1954; and the U.N.S.M. example, by C. Bertrand Schultz and associates, 1934.

Forty-eight specimens are here recorded:

[1] Includes 46 F:A.M. and 2 U.N.S.M. specimens.

[2] Named in honor of H. R. Wanless who made a comprehensive study of the Oligocene deposits of South Dakota.

HOLOTYPE

Skull with I^1–M^3 and mandible with I_1–/C rt. and P_1–M_3. (w+)	F:A.M. 72014	From oreodont faunal "Zone D" of Brule Formation, head of Spring Creek, SE. of Sheep Mountain, White River drainage, Shannon County, South Dakota; collected by Gordon Fletcher, Ralph Mefferd, and Morris F. Skinner, 1938 Figures 6–9

REFERRED FROM (A) SHANNON, (B) PENNINGTON, (C) WASHABAUGH, (D) JACKSON, AND (E) FALL RIVER COUNTIES, SOUTH DAKOTA; (F) GENERAL AREA, SOUTH DAKOTA; AND (G) SIOUX COUNTY, NEBRASKA

A. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM SW. SIDE OF SHEEP MT.:

SKULL		F:A.M.
Partial skull with P^1–P^2 rt. and P^3(br.)–M^3	(w‡+)	45296

FROM $\frac{3}{4}$–$1\frac{1}{4}$ MI. S. OF COTTONWOOD PASS[1] (BIG CORRAL DRAW AREA):

SKULL AND MANDIBLE		
Skull with C/–P^1 br. and P^2–M^3 and mandible with I_1–M_3	(w)	72075

The above specimen is larger than average examples of this species.

SKULL		
Skull with C/–M^3	(w‡)	45288

FROM S. OF COTTONWOOD PASS, E. FORK BIG CORRAL DRAW:

3 SKULLS AND MANDIBLES (ATTACHED)		
Partial skull with I^1–M^3 (I^2–C/ br.) and mandible with I_2–M_3 (P_1 br.)	(w)	45321
Skull with I^1(alv.)–dP^2–M^3(germ) and mandible with I_1–I_2 br. and I_3–dP_3–M_2	(I)	72021
Inferior portion of skull with I^2–M^3 and mandible (attached) with I_1(rt.)–M_3	(w‡)	72088

4 SKULLS		
Skull with I^1–I^3 rt. and C/(br.)–M^3 (P^1–P^3 br.)	(w+)	72022
Partial skull with P^4–M^3	(w)	72023
Partial skull with P^1(rt.)–dP^3–M^3	(I)	72078
Partial skull with P^1–M^3 br.	(w‡+)	72278

B. FROM WHITE RIVER DRAINAGE, NORTH SIDE OF PINNACLES, PENNINGTON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBULAR RAMUS		F:A.M.
Partial skull with P^1–M^3(br.) and partial right ramus with M_2–M_3 br.	(w)	72025

B'. FROM CHEYENNE RIVER DRAINAGE, FIRST CANYON NORTH OF SCHOOL OF MINES CANYON, WEST SIDE OF SHEEP MOUNTAIN, PENNINGTON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE		F:A.M.
Skull with I^1–M^3 and mandible with I_1–M_3	(w)	72148

FROM W. BIG CORRAL DRAW:

SKULL		
Skull with C/–P^1 rt. and P^2–M^3	(w+)	45325

A'. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM HEAD OF WIND CREEK, E. AND S. OF SHEEP MT.:

[1] The Cottonwood Pass area is in the region between the Cheyenne River and White River drainages.

4 SKULLS AND MANDIBLES (ATTACHED)		F:A.M.
Partial skull with P^3–M^3 and partial mandible with P_1–P_3 br. and P_4–M_3	(w+)	45284
Partial skull with P^4–M^3 and partial mandible with P_4–M_3	(w)	72015
Skull with C/(alv.)–M^3 and mandible with I_3–P_2 rt. and P_3–M_3	(w‡)	72076
Partial skull with C/(br.)–M^3 and mandible with P_1(rt.)–M_3	(w+)	72082

MANDIBULAR RAMUS

Partial right ramus with P_3–M_3	(w+)	72280

FROM HEAD OF SPRING CREEK, SE. OF SHEEP MT.:

2 SKULLS AND MANDIBLES

Skull with I^1(rt.)–M^3 and mandible with I_1–M_3	(w‡)	72094
Skull with C/–M^3 and mandible (attached) with P_1(rt.)–M_3	(w‡)	72309

2 SKULLS

2 partial skulls with		
C/(rt.)–M^3 (P^1 br.)	(w)	72016
C/–P^2 rt. and P^3(br.)–M^3	(w‡)	72017

FROM SE. CORNER OF SHEEP MT.:

SKULL

Partial skull with P^2–P^4 br. and M^1–M^3	(w+)	72018

FROM SE. OF COTTONWOOD PASS:

SKULL

Partial skull with C/–M^3 (P^1 alv. and P^2 br.)	(w)	72024

C. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM HAY CREEK AREA:

SKULL AND MANDIBLE		F:A.M.
Partial skull with C/–P^3 rt. and P^4–M^3 and mandible with I_1–I_2 rt. and I_3–M_3 (/C alv.)	(M+)	72026

3 SKULLS

Partial skull with I^1(rt.)–M^3 (I^1–I^2 and P^2–P^4 br.)	(w‡)	45293
Partial skull with C/(rt.)–M^3 (P^1 br.)	(M)	45294
Skull with C/(rt.)–dP^2–M^3(germ)	(I)	72077

FROM POTATO CREEK BASIN:

MANDIBLE, IMMATURE

Partial mandible with /C–P_2 rt. and dP_3–M_3(br., erupt.)	(I)	72279

FROM E. SIDE OF POTATO CREEK:

SKULL

Skull with I^3(rt.)–M^3 (P^2 br.). Figure 52 (in part)	(w+)	72109

FROM 1 MI. N. OF QUIVER HILL, 18 MI. S. OF KADOKA:

SKULL AND HUMERUS

Partial skull with M^3 br. and partial humerus. Figure 19 (in part)	(M)	72028

D. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA,[1] JACKSON COUNTY, SOUTH DAKOTA

FROM ½–1 MI. E. OF CEDAR PASS:

[1] The Cedar Pass area is in the divide region between the White River and Bad River drainages.

2 SKULLS AND MANDIBULAR RAMI		F:A.M.
Partial skull with P^1–M^3 and partial left ramus with M_1–M_3(br.)	(W)	72029
Skull with dP^2(rt.)–M^3(erupt.) and mandible with /C–dP_2–M_3(erupt.)	(I)	72030

SKULL

Partial skull with C/(br.)–dP^3–M^3 (P^2 alv.)	(I)	72033

FROM ¼–1¼ MI. W. OF CEDAR PASS:

SKULL AND MANDIBLE

Partial right side of skull with dP^4–M^3(erupt.) and partial mandible with P_1–dP_2 br. and dP_3–M_3(erupt., br.)	(I)	72231

3 SKULLS

3 partial skulls with		
P^1 and M^1–M^3	(M+)	72032
C/(br.)–M^3	(W‡)	72034
dP^3(br.)–M^3(br. and erupt.)	(I)	72036

FROM ½–2½ MI. NE. OF CEDAR PASS:

SKULL AND MANDIBLE, IMMATURE

Partial skull with C/–dP^3–M^3(erupt.) (P^2 and M^1 rt., dP^4 br.) and mandible with /C–dP_2–M_3 (P_1–dP_2 br.)	(I)	72149

3 SKULLS

3 partial skulls with		
I^1–I^2 alv. and I^3–M^3	(W+)	45299
P^2–M^3	(M)	45301
I^3–C/ rt. and P^1–M^3	(W+)	72035

FROM TOP OF HILL ON PASS, 3½–4 MI. NW. OF INTERIOR:

SKULL

Partial skull with C/(rt.)–M^3	(W‡+)	45291

The field data accompanying the above specimen indicate that it came from the "upper part of Upper *Oreodon* or Lower *Leptauchenia* zone." The specimen is here considered as coming from the latter.

FROM N. OF INTERIOR:

SKULL

Partial skull with P^3–M^3	(W‡)	45300

E. FROM WHITE RIVER DRAINAGE, LITTLE BAD LANDS, OELRICHS, FALL RIVER COUNTY, SOUTH DAKOTA (COLLECTED BY ALBERT THOMSON, 1940)

SKULL		A.M.
Partial skull with C/(rt.)–M^3 (P^1 br. and P^2 rt.)	(W)	39120

F. FROM GENERAL AREA,[1] SOUTH DAKOTA, 1892

SKULL AND MANDIBLE (ATTACHED)		A.M.
Partial skull with C/(br.)–M^3 and mandible with P_1–M_3	(W)	613

G. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, U.N.S.M. COLL. LOC. SX-9, SIOUX COUNTY, NEBRASKA

SKULL		U.N.S.M.
Skull with C/–M^3	(W+)	28470

[1] Exact geographic locality unkown.

2. Paramerycoidodon (Gregoryochoerus) meagherensis (Koerner)

From deposits approximately equal in age to the Gering Formation, Meagher County, Montana; and tentatively referred remains from Gering Formation, Morrill County, Nebraska

Eporeodon meagherensis KOERNER, 1940, p. 845, pl. 2, figs. 1–3, pl. 3.

CHARACTERS

SKULL: Medium size, average-sized examples larger than those of *P.* (*G.*) *wanlessi;* bulla more oblong (anteroposteriorly) than in examples of *P.* (*G.*) *wanlessi.*

MANDIBLE: Larger than examples of *P.* (*G.*) *wanlessi;* inferior border of ramus sloping noticeably downward posteriorly [more as in examples of *P.* (*B.*) *major*]; ascending ramus wide (anteroposteriorly), wider and higher than examples of *P.* (*G.*) *wanlessi*; condyle set at nearly a right angle to longitudinal axis of premolar-molar series, with external border more anterior than internal.

DENTITION: Larger (especially premolars) than in examples of *P.* (*G.*) *wanlessi;* premolars slightly crowded but less so than examples of *P.* (*G.*) *wanlessi;* P^1–P^4 each with weak anterior intermediate crest; anterior and posterior crests of molars more upright than in examples of *P.* (*G.*) *wanlessi* and other Oligocene species of the Merycoidodontinae (in Oligocene forms, anterior and posterior crests of superior molars sloping inward and downward; in Miocene forms, crests more perpendicular); P_3 and P_4 each with a posterior intermediate crest, weaker in P_4 than in P_3.

LIMBS: More robust than examples of *P.* (*G.*) *wanlessi.* (Known only from incomplete elements.)

MEASUREMENTS: Tables 3 and 7 (pp. 84 and 146).

ILLUSTRATIONS: Figures 6, 7, 9, 52.

DISCUSSION

Koerner[1] described this species under the genus *Eporeodon* and made comparisons with *E. pacificus* and stated: "*Eporeodon meagherensis* is closer to *E. pacificus* than to any of the other species of *Eporeodon.* In fact, it is quite possible that the discovery of more material may prove that it should be considered a subspecies of *E. pacificus* . . . Finally, the lacrimal fossa is shallower than that of the latter species."

The present writers consider that the two forms in question differ considerably. Examples of *Eporeodon* (*Paraeporeodon*) *pacificus* superficially resemble those of *P.* (*G.*) *meagherensis* but differ as follows: *P.* (*G.*) *meagherensis* possesses lighter occipital condyles, smaller bullae, smaller and lighter postglenoid processes (lacking the pronounced inward and downward slope of the external border), smaller and shallower lacrimal fossae, and more robust dentitions.

The light dentitions of the Eporeodontinae are similar to examples of the *Genetochoerus* and *G.* (*Osbornohyus*) phylum, but are much lighter than other examples of the Merycoidodontinae. [See discussion of *E.* (*P.*) *pacificus,* p. 205.]

The geologic occurrence of both forms should be considered. The John Day deposits are here considered to be approximately equal in age to the Harrison of the Great Plains, whereas the deposits yielding remains of *P.* (*G.*) *meagherensis* are thought to be equivalent to the Gering in age. (See discussion of John Day deposits, p. 194.)

The F:A.M. specimen was collected by Charles H. Falkenbach and associates, 1942; and the U.N.S.M. example, by Bertrand Schultz and associates, 1933.

Three specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_2–M_3, partial radius, partial ulna, partial manus, and hyoid. (w)	Y.P.M. 13948	From deposits approximately equal in age to the Gering Formation, sect. 17, T. 11, R. 5 E., Meagher County, Montana; collected by Koerner Figured by Koerner, 1940, pl. 2, figs. 1–2, pl. 3

[1] 1940, p. 845.

TABLE 4

Otionohyus, NEW GENUS, AND *Otionohyus* (*Otarohyus*), NEW SUBGENUS. COMPARATIVE MEASUREMENTS[a] OF SKULLS AND MANDIBULAR RAMI

SKULL	*O. wardi*, new species	*O. wardi degrooti*, new subspecies	?*O. vanderpooli*, new species	*O.* (*O.*) *bullatus* (Leidy)		*O.* (*O.*) *cedrensis* (Matthew)	
	Holotype F:A.M. 49662	Holotype F:A.M. 49760	Holotype F:A.M. 49766	Holotype A.N.S.P. 10681	Referred F:A.M. 45267	Holotype A.M. 8949	Referred F:A.M. 45272
Stage of wear of teeth	(W‡)	(W+)	(M+)	(W)	(W+)	(I)	(W+)
Length (incl. supraoccipital crest and incisors)	178	185	(187)	((200))	((200))	—	—
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	163	164	(169)	((185))	((180))	163.5	((175))
Width (max.)	106	94.5	(99)	((115))	((104))	((102))	(119)
Width of brain case (max.)	51.5	45	54.5	55	55	52	57.5
Width, interorbital (min.)	52	49	50.5	52.5	53	—	51.5
Distance from anterior rim of orbit to anterior base of C/	71	68.5	72.5	72.5	76	68	—
Distance from anterior rim of orbit to supraoccipital crest	118.5	115.5	(110)	((135))	((130))	—	((118))
Length of nasals	(72.5)	(74)	—	—	((73))	—	—
Width of muzzle at infraorbital foramina	48	40	42	—	48	42.5	45
Width across canines	48	(28)	19.5	—	39.5	40.5	—
Length, C/–M^3 incl.	95	88	95.5	97.5	97	—	—
Length, P^1–M^3 incl.	85	80	84.5	84.5	83.5	—	82
Length, P^1–P^4 incl.	40	36.5	41.5	42.5	42	45[b]	39
Length, M^1–M^3 incl.	47	44.5	45	45	43	—	46.5
Width of M^3 (max.)	18.5	18	19	19	18	—	13
Depth of malar below orbit	16.5	14	14	15	16.5	17	16

TABLE 4—(*Continued*)

MANDIBULAR RAMUS	*O. wardi*, new species	*O. wardi degrooti*, new subspecies	?*O. vanderpooli*, new species	*O.* (*O.*) *bullatus* (Leidy)		*O.* (*O.*) *cedrensis* (Matthew)	
	Holotype F:A.M. 49662	Holotype F:A.M. 49760	Holotype F:A.M. 49766	Holotype A.N.S.P. 10681	Referred F:A.M. 45267	Holotype A.M. 8949	Referred F:A.M. 45272
Length (max., incl. incisors)	—	159.5	—	—	—	147.5	—
Length, /C-condyle incl.	—	142.5	—	—	—	136.5	—
Depth of jaw under coronoid	—	73.5	—	—	—	59.5	—
Depth of jaw below anterior edge of M_3	34	32.5	—	—	30	31.5	—
Length, /C–M_3 incl.	—	96	—	—	—	—	—
Length, P_1–M_3 incl.	((89))	87	—	—	((90))	—	—
Length, P_1–P_4 incl.	40.5	37.5	—	—	(41.5)	47[b]	—
Length, M_1–M_3 incl.	((48.5))	50.5	—	—	48.5	—	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] Includes dP-dP.

REFERRED FROM (A) MEAGHER COUNTY, MONTANA; AND TENTATIVELY REFERRED FROM (B) SIOUX COUNTY, NEBRASKA

A. FROM WHITE SULPHUR SPRINGS AREA, MEAGHER COUNTY, MONTANA

SKULL AND MANDIBLE

Skull with C/(rt.)–M^3(br.) and mandible with /C–P_1 br. and P_2–M_3. Figures 6, 7, 9, 52	(w‡)	F:A.M. 45462

B. TENTATIVELY REFERRED FROM NORTH PLATTE RIVER DRAINAGE, U.N.S.M. COLL. LOC. MO–111, MORRILL COUNTY, NEBRASKA

SKULL

		U.N.S.M.
Skull with C/(rt.)–M^3	(w+)	28623

III. **OTIONOHYUS**, NEW GENUS

GENOTYPE: *Otionohyus wardi*, new species.

DESCRIPTION

SKULL: Small size, smaller than examples of *Merycoidodon, Paramerycoidodon* or their subgenera; moderately low and flat; basal lengths ranging from 156 to 173 mm., widths from 94 to 108 mm.; approaching mesocephalic; facial region lowest of subfamily; supraoccipital wings well extended posteriorly beyond occipital condyles; sagittal crest moderately low to prominent [higher in *O.* (*Otarohyus*)]; brain case moderately inflated; frontals flat; nasals moderately broad, posterior border acute to obtuse; orbit moderately small [larger in *O.* (*Otarohyus*)], roundish, looking outward and slightly forward and upward; malar moderately shallow below orbit; zygomatic arch moderately light; infraorbital foramen in area above posterior portion of P^2 to posterior portion of P^3; lacrimal fossa moderately large and deep; premaxillae touching but not joined; occipital condyles moderately light; paroccipital process light, anterior-external surface excavated; bulla small (minute) [inflated in examples of *O.* (*Otarohyus*)]; postglenoid process moderately light [heavier in examples of *O.* (*Otarohyus*)], wider laterally than anteroposteriorly, external border sloping down and inward, less inward slope than in examples of *Merycoidodon, Paramerycoidodon,* and their subgenera.

MANDIBLE: Moderately light; postsymphysis in area below posterior portion of P_3; ramus moderately shallow (less depth than in examples of *Merycoidodon, Paramerycoidodon,* and their subgenera); condyle moderately large, comparable with that of *Merycoidodon.*

DENTITION: Series small and light, smaller and lighter than examples of *Merycoidodon* and its subgenera, and decidedly lighter and smaller than dentitions of *Paramerycoidodon* and its subgenera, more massive than those of *Genetochoerus* (from same faunal zone); P^1–P^4 each with anterior intermediate crest, weak on P^4; P_2–P_3 each usually with light posterior intermediate crest.

LIMBS: Short and light, shorter and lighter than examples of *Merycoidodon, Paramerycoidodon,* and their subgenera; approximate size of those of *Genetochoerus.*

MEASUREMENTS: Tables 4 and 7 (pp. 104 and 146.)

ILLUSTRATIONS: Figures 10, 11, 52 (skulls, mandibles, and dentitions), 19–23 (limbs).

DISCUSSION

Remains of *Otionohyus* have skulls that are smaller than examples of *Merycoidodon, Paramerycoidodon,* and their subgenera. The basal lengths of the skulls of *Otionohyus* are approximately equal to those of *Genetochoerus.* The skulls, however, are lower and flatter than in other genera of the Merycoidodontinae.

The inclusion of skulls that are low and flat with those that are comparatively high and narrow in one subfamily was also noted in the Phenacocoelinae[1] (*Phenacocoelus* "skulls low to moderately high," and *Hypsiops* skulls "high") and in the Miniochoerinae[2] (*Platyochoerus* skulls "low," and *Stenopsochoerus* skulls "high"). In each instance, however, the primary subfamily characters are present and are evident in both the low and high skulls.

It is here considered that *Otionohyus* gave rise to *O.* (*Otarohyus*), with the major difference being the minute bullae of *Otionohyus* and the inflated bullae of the subgenus.

[1] Schultz and Falkenbach, 1950, pp. 101, 113.
[2] *Idem,* 1956, pp. 427, 435.

The proposed sequence of the species of *Otionohyus* is as follows: *O. wardi degrooti* from "Zone C" of the Chadron, and *O. wardi* from "Zone A" of the Brule. *?Otionohyus vanderpooli* is also from "Zone C" of the Chadron.

Distribution

Two species and one questionably referred species of *Otionohyus* are known from the upper Chadron (oreodont faunal "Zone C" of the Chadron) and lower Brule (oreodont faunal ("Zone A"), of Nebraska, North Dakota, South Dakota, and Wyoming. (See geologic distribution chart, p. 22.)

Summary of Species and Types

Two species and a questionably referred species of *Otionohyus* from 10 Chadron (oreodont faunal "Zone C") and Brule ("Zone A") localities are here recorded:

1. *Otionohyus wardi,* new species, from Sioux County, Nebraska; referred remains from Sioux, Scotts Bluff, and Dawes counties, Nebraska; Niobrara and Converse counties, Wyoming; Shannon, Pennington, and Harding counties, South Dakota; and Stark County, North Dakota. ("Zone A" of Brule.)

Holotype: Skull, mandible, and skeletal elements, F:A.M. 49662. Figures 10, 11, 19, 20, 22, 23.

1a. *Otionohyus wardi degrooti,* new subspecies, from Converse County, Wyoming; referred remains from Niobrara County, Wyoming; Dawes County, Nebraska; and Fall River County, South Dakota. ("Zone C" of Chadron.)

Holotype: Skull, F:A.M. 49760. Figures 10, 11, 19–23, 52.

2. *?Otionohyus vanderpooli,* new species, from Sioux County, Nebraska. ("Zone C" of Chadron.)

Holotype: Skull and skeletal elements, F:A.M. 49766. Figures 10, 19, 22.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS

OTIONOHYUS

Total available specimens: 108[1]

1. **Otionohyus wardi,**[2] new species

From "Zone A" of the Brule Formation, Sioux County, Nebraska; referred remains from Sioux, Scotts Bluff, and Dawes counties, Nebraska; Niobrara and Converse counties, Wyoming; Shannon, Pennington, and Harding counties, South Dakota; and Stark County, North Dakota

Description

Skull: Smallest examples of Merycoidodontinae except for those of *Genetochoerus-G.* (*Osbornohyus*) phylum; posterior border of nasal mostly acute. (See generic description.)

Mandible: Same size comparisons as for skull; comparatively light (more like examples of *Genetochoerus periculorum*); ascending ramus shallower than examples of *Merycoidodon* or *Paramerycoidodon* (similar to those of *G. periculorum*). (See generic description.)

Dentition: (See generic description.)

Limbs: Shorter and lighter than examples of *Merycoidodon* and *Paramerycoidodon,* length comparable, but more massive than examples of *G. periculorum.*

Measurements: Tables 4 and 7 (pp. 104 and 146).

Illustrations: Figures 10, 11, 19–23, 52.

Discussion

Remains of *Otionohyus wardi* from "Zone A" of the Brule and those of *O. w. degrooti* from "Zone C" of the Chadron have skulls that are approximately equal in length to those of *Genetochoerus periculorum* (smallest of the Merycoidodontinae). The former two, however, have wider skulls and more massive dentitions.

Some characters of *O. wardi* (size of skull and length of limbs) are typical of *Otionohyus;* other characters (massive teeth and robust limbs) approach those of *M. culbertsonii.* The lower and flatter skulls of *Otionohyus-O.* (*Otarohyus*), however, represent a phylum independent of *Merycoidodon.*

It is here considered that *O. wardi* was derived from *O. w. degrooti* of "Zone C" of the

[1] Includes 75 F:A.M. and 22 U.N.S.M. specimens.

[2] Named in honor of N. Z. Ward, a collector for the Frick Laboratory for more than 20 years.

Chadron, and in turn gave rise to *O.* (*Otarohyus*) *bullatus* of "Zone B" of the Brule.

There are two skulls, F:A.M. 45099 and 45100, referred to this species, but the associated geological data are questioned by the present writers. Both specimens are among the first Oligocene oreodonts collected by Morris Skinner and Ralph Mefferd of the Frick Laboratory in South Dakota and have field data placing them both in the "Middle *Oreodon* beds" (="Zone B" of the Brule). However, both skulls have small (minute) bullae which in all other examples of this subfamily are found below "Zone B" of the Brule. In the Desmatochoerinae the minute bullae also are restricted to forms from below faunal "Zone B" of the Brule. There is, of course, the possibility that there was an error in identifying the stratigraphic zone for the two specimens during the first two weeks that the field party collected in the region; or perhaps the skulls were inadvertently mislabeled in the field or laboratory. On the other hand it is also possible, but not probable, that a few oreodonts with small bullae survived as "living fossils" into the early part of faunal "Zone B" time.

The F:A.M. material from Nebraska was collected by Morris F. Skinner, Charles H. Falkenbach, and associates, 1944; from Wyoming, by Charles H. Falkenbach and associates, 1938, 1943, 1945, 1948, and 1954; from South Dakota, by Morris F. Skinner and associates, 1938–1940, 1944, 1945; from North Dakota, by Morris F. Skinner and associates, 1944. The U.N.S.M. material was collected by C. Bertrand Schultz and associates, 1933–1941. The A.M. example was collected by Albert Thomson and Walter Granger, 1941.

One hundred and three specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3(rt.) (M_2 br.), partial scapula, 2 humeri, 2 radii, 2 ulnae, 2 partial manus, partial femur, 2 partial tibiae, partial pes, vertebrae, and ribs. (w‡)	F:A.M. 49662	From oreodont faunal "Zone A" of Brule Formation, E. end of exposures N. of Harrison,[1] Hat Creek Basin, Cheyenne River drainage, Sioux County, Nebraska; collected by Ove Kaisen and Charles H. Falkenbach, 1944 Figures 10, 11, 19, 20, 22, 23

REFERRED FROM (A) SIOUX, (B) SCOTTS BLUFF, AND (C) DAWES COUNTIES, NEBRASKA; (D) NIOBRARA AND (E) CONVERSE COUNTIES, WYOMING; (F) SHANNON, (G) PENNINGTON, AND (H) HARDING COUNTIES, SOUTH DAKOTA; AND (I) STARK COUNTY, NORTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NORTH OF HARRISON, SIOUX COUNTY, NEBRASKA

2 SKULLS, MANDIBLE (ATTACHED), AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with C/–M^3, mandible with I_1–M_3, 2 partial manus, partial tibiae, and astragalus	(M+)	72037
Partial skull with C/–M^3, mandible with I_1–M_3, partial scapula, 2 partial humeri, partial ulna, and fragments	(W)	72038

2 SKULLS AND MANDIBULAR RAMI

Partial skull with P^2–M^3 and partial left ramus with M_2(br.)–M_3	(w‡)	49583
Partial skull with C/–dP^2–M^3(germ) and mandible with /C–dP_2–M_3(germ)	(I)	49664

SKULL

Partial skull with I^1–M^3 (I^3 rt.)	(M)	72039

FROM U.N.S.M. COLL. LOC. SX–4:

3 SKULLS AND MANDIBLES (ATTACHED)

		U.N.S.M.
Partial skull with C/(rt.)–dP^2–M^3(erupt.) and mandible with P_1–dP_2–M_3(erupt.)	(I)	28146

[1] Area of U.N.S.M. Coll. Loc. 6 and 7.

		U.N.S.M.
Partial skull with P^1–M^3 and mandible with P_1(rt.)–M_3	(w+)	28063
Partial skull with I^1–I^2 br. and I^3–dP^2–M^2 (C/ erupt.) and partial mandible with I_1–/C br. and P_1–dP_2–M_2	(I)	28274

SKULL

Partial skull with P^1–M^3	(w‡⁺)	28075

FROM AREA OF U.N.S.M. COLL. LOC. SX–4 AND 5:

SKULL

Partial skull with C/(rt.)–M^3 and partial right ramus with P_4(br.)–M_3	(w+)	28188

FROM U.N.S.M. COLL. LOC. SX–5:

SKULL

Partial skull with I^1–M^3	(w+)	28034

FROM U.N.S.M. COLL. LOC. SX–6:

SKULL AND MANDIBLE (ATTACHED)

Skull with I^1–I^2 rt. and I^3–M^3 (C/ br.) and mandible with P_1(br.)–M_3	(w‡)	28473

5 SKULLS

Partial skull with I^1–I^2 rt. and I^3–M^3	(w+)	28059
Partial skull with C/–M^3	(w‡)	28196
Partial skull with I^1–C/ rt. and P^1–M^3	(w)	28288

The above skull has an additional tooth embedded crosswise in the palate, and the crown surface has grown against the right C/ and turned downward, and shows wear.

Skull with I^1–M^3 (I^3–C/ br.)	(w‡)	28471
Partial skull with I^1–P^1 rt. and P^2–M^3	(w‡)	28472

FROM U.N.S.M. COLL. LOC. SX–37:

SKULL

Partial skull with C/–P^1 rt., P^2–P^4 erupt. and M^1–M^3(erupt.)	(I)	28199

A′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–24:

2 SKULLS AND MANDIBLES

		U.N.S.M.
Anterior portion of skull with C/(rt.)–M^3 (P^1 br.) and partial mandible with /C–P_1 rt. and P_2–M_3	(w)	28277
Partial skull with P^1–dP^2–M^2 and mandible (attached) with dP_2–M_2	(I)	28161

FROM U.N.S.M. COLL. LOC. SX–31:

2 SKULLS

Partial skull with C/(br.)–M^3.	(–M)	28192
Skull with I^1–dP^2–M^3(germ)	(I)	28204

FROM E. OF U.N.S.M. COLL. LOC. SX–31:

SKULL (IMMATURE)

Partial skull with C/–P^1 rt. and dP^2–M^3(erupt.)	(I)	28127

FROM U.N.S.M. COLL. LOC. SX–32:

SKULL AND MANDIBLE

Partial skull with P^1–M^3 and mandible with I_1–/C rt. and P_1(alv.)–M_3	(w+)	28179

B. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SF–101:

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Partial skull with P^1–M^3 and mandible with P_1–M_3	(W+)	28142

SKULL		
Partial skull with I^1–P^1 rt. and P^2–M^3	(M)	28198

FROM U.N.S.M. COLL. LOC. SF–102:

SKULL		
Skull with C/(rt.)–dP^2–M^2	(I)	28040

C. FROM WHITE RIVER DRAINAGE, 4 MILES NORTHEAST OF CHADRON,[1] DAWES COUNTY, NEBRASKA

MANDIBULAR RAMUS		F:A.M.
Partial left ramus with P_1–M_1(br.)	(W)	72224

D. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SHACK DRAW AREA:

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS		F:A.M.
Skull with I^1(rt.)–M^3 (C/, P^1 and M^2–M^3 br.), mandible (attached) with I_1–/C rt. and P_1–M_3, partial humerus, 2 radii (1 partial), partial ulna, 2 partial manus, and vertebrae	(W+)	49654

SKULL, MANDIBULAR RAMUS, AND SKELETAL ELEMENTS		
Anterior portion of skull with I^1–M^3, partial left ramus with /C(br.)–M_3, 2 radii, 2 ulnae, and partial manus. Figure 23 (in part)	(W‡)	72040

3 SKULLS AND MANDIBLES		
Partial skull with P^1(rt.)–M^3 and mandible with I_3–M_3 (/C–P_1 rt.)	(M)	72041
Partial right premaxilla and maxilla with I^1–I^2 rt. and I^3–C/(br.)–P^2(rt.) (P^1 rt.) and partial mandible with I_1–M_3	(W)	72042
Partial skull with I^1(rt.)–M^3 and mandible (attached) with I_1–M_3	(W‡)	72228

8 SKULLS		
8 partial skulls with		
C/–P^1 rt. and P^2–M^3	(W+)	45014
P^1–P^2 rt. and P^3(br.)–M^3	(W‡)	45027
I^1–M^3	(W‡)	45094
C/(rt.)–M^3. Figure 52	(M+)	45015
C/(rt.)–M^3	(W)	45102
I^1–I^3 rt. and C/–M^3	(M+)	45103
P^1–M^3	(W)	72043
C/–M^3	(–M)	72313

FROM SW. END OF SEAMEN HILLS:

SKULL AND MANDIBLE (ATTACHED)		
Anterior, inferior portion of skull with P^2–M^3 (M^1–M^2 br.) and partial mandible with /C–P_1 rt. and P_2–M_3	(W+)	72282

The above is the lowest geological occurrence of the species, from the base of the "Purplish White" layer.

FROM SPRING DRAW:

[1] U.N.S.M. Coll. Loc. DW-105.

SKULL AND MANDIBLE

		F:A.M.
Partial skull with P^1–M^1 rt. and M^2–M^3 and partial mandible with I_1–I_3 rt. and /C(br.)–M_3 (P_1 br.)	(w‡‡)	45091

3 SKULLS

Partial skull with C/(rt.)–M^3(br.) (P^1–P^2 rt.)	(w‡)	45016
Partial skull with I^1(rt.)–M^3	(w+)	45029
Partial skull with P^1–dP^2–M^2	(I)	72249

FROM SE. OF SPRING DRAW AREA (KLEMKE RANCH):

2 SKULLS

Skull with I^1–I^2 rt. and I^3–M^3 (C/ br.)	(M+)	72044
Anterior portion of skull with I^1–dP^2–M^1 (dC/ present and C/ erupt.)	(I)	72045

FROM OLD WOMAN CREEK:

SKULL AND MANDIBLE (ATTACHED)

Inferior portion of skull with P^1–M^3 and mandible with I_1–I_3 rt. and /C(br.)–M_3	(w)	45081

SKULL

Partial skull with I^1–M^3 (C/ rt.)	(w+)	45060

FROM DUE NORTH OF NODE:

SKULL

Skull with I^1–I^3 alv. and C/–M^3.	(M+)	72046

E. FROM NORTH PLATTE RIVER DRAINAGE, 6 MILES SOUTHEAST OF DOUGLAS, CONVERSE COUNTY, WYOMING

2 SKULLS AND MANDIBLES

		F:A.M.
Skull with I^1–I^3 br. and C/–dP^3–M^3(erupt.) and mandible with /C–P_1 br. and P_2–dP_3–M_3(erupt.)	(I)	49658
Skull with I^1–I^3 rt. and C/–dP^3 and partial mandible with I_1–dP_3–M_2	(I)	72250

SKULL AND SKELETAL ELEMENTS

Skull with I^3–M^3, partial scapula, humerus, and partial tibia	(w)	72047

F. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM INDIAN CREEK, 1½–3 MI. W. OF SHEEP MT.:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Skull with I^2–M^3, mandible with I_1–M_3, 2 partial scapulae, 2 humeri (1 partial), 2 partial radii, partial ulna, 2 femora, 2 tibiae (1 partial), 2 astragali, partial calcaneum, and vertebrae. Figure 21 (in part)	(–M)	45044

5 SKULLS AND MANDIBLES (ATTACHED)

Partial skull with P^1(br.)–M^3 and partial mandible with P_4–M_3	(w‡)	45046
Partial skull with I^3(alv.)–M^3 (C/ rt.) and partial mandible with P_3–M_3	(w+)	45225
Partial skull with I^3–C/ rt. and P^1–M^3 (P^3 br.) and partial mandible with P_3–M_3	(w+)	45257
Anterior portion of skull with C/–P^1 rt. and dP^3–M^3(erupt.) and partial mandible with I_1–P_1 rt. and dP_2–M_3(erupt.)	(I)	72221
Skull with C/–dP^2–M^3(erupt.) and mandible with I_3–/C br. and P_1–dP_2–M_3(erupt.)	(I)	72256

SKULL

Skull with C/–M^3	(w+)	72048

MANDIBLE F:A.M.

Partial mandible with I_1–P_1 rt. and P_2–M_3 (P_3 rt.) . . . . (w+) 72222

FROM N. OF SHEEP MT.:

MANDIBLE

Partial mandible with I_1–/C rt. and P_1–dP_2–M_2 . . . . (I) 72223

FROM W. SIDE OF SHEEP MT.:

MANDIBULAR RAMUS

Partial right ramus with I_1–P_2 rt. and P_3–M_3 . . . . (w) 72261

FROM $1\frac{1}{2}$ MI. S. OF COTTONWOOD PASS (BIG CORRAL DRAW AREA)[1]:

SKULL AND MANDIBLE

Skull with I^3–dP^2–M^3(erupt.) and mandible with I_1–dP_2–M_3(erupt.) (I_2 and /C br.) . . . . (I) 72264

FROM N. OF COTTONWOOD PASS (BIG CORRAL DRAW AREA):

SKULL

Skull with I^1–I^3 alv. and C/–M^3 (P^1 br.) . . . . (w) 45233

FROM $\frac{1}{2}$ MI. N. OF COTTONWOOD PASS (BIG CORRAL DRAW AREA):

SKULL

Partial skull with I^1–I^3 alv. and C/–M^3 . . . . (w) 45100

The field data show that the above specimen was from "20′ above top of lower nodules, middle Oreodon beds." The bullae are small (minute), and the skull is typical of those from "Zone A" of the Brule. (See discussion, p. 27.)

FROM BIG CORRAL DRAW:

2 SKULLS AND MANDIBLES

Partial skull with I^2–C/ rt. and P^1(br.)–M^3 and partial mandible with I_1–I_3 br. and /C–M_3 . . . . (w) 45095

Partial skull with C/(rt.)–M^3 and mandible (attached) with I_1–I_3 br. and /C(alv.)–M_3 (P_1 br.) . . . . (w‡) 45256

SKULL

Partial skull with I^3–C/ rt. and P^1–M^3 (P^1 br.) . . . . (w‡) 45104

2 MANDIBLES

Partial mandible with I_1–P_2 rt. and P_3–M_3 . . . . (w) 72164

Partial mandible with I_1–M_3 (M_1 br.) . . . . (w) 72253

G. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM 2 MI. E. AND $\frac{1}{2}$ MI. S. OF IMLAY:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P^1–M^3, mandible (attached) with P_1(br.)–M_3, and partial humerus . . . . (w‡) F:A.M. 45213

FROM $\frac{3}{4}$–1 MI. W. OF IMLAY:

SKULL AND MANDIBLE (ATTACHED)

Skull with I^1–M^3 and mandible with I_1–M_3 . . . . (w‡) 45255

[1] The Cottonwood Pass localities are on the divide region between the Cheyenne River and White River drainages.

		F:A.M.
SKULL		
Partial skull with P^3–M^3	(M+)	45043

FROM 7½ MI. W. OF CONATA:

MAXILLA AND MANDIBLE		
Partial right maxilla with P^2–M^3 and partial mandible with P_2(rt.)–M_3	(W+)	72276
SKULL		
Partial skull with I^2(rt.)–M^3 (I^3 alv. and C/ rt.)	(W)	45071

FROM 2 MI. S. OF CONATA:

MANDIBLE		
Partial mandible with P_4–M_3	(W)	72220

FROM 4 MI. SE. OF SCENIC:

6 SKULLS AND MANDIBLES		
Partial skull with I^1–I^3 rt. and C/(br.)–M^3 (P^1–P^2 br.) and partial mandible with I_1–P_2 rt. and P_3–M_3	(W+)	45020
		A.M.
Skull with I^1–M^3 (C/ br.) and mandible with I_1(rt.)–M_3 (I_3 rt.)	(M+)	39118
Skull with I^1–M^3 and mandible (attached) with I_1–M_3	(W)	39434
Skull with I^1–C/ rt. and P^1–M^3 and mandible with I_1–M_3	(W)	39436
Skull with I^1–M^3 and mandible (attached) with I_1–M_3	(W‡)	39458
Partial skull with I^1–M^3 (M^2 br.) and mandible (attached) with I_1(alv.)–M_3	(W+)	48818
SKULL		
Partial skull with I^1–C/ rt. and P^1–M^3(br.)	(W+)	39456

FROM MILLER BASIN, CAIN CREEK AREA:

2 SKULLS		
Partial skull with I^2–C/ rt. and P^1–M^3	(W+)	45038
Partial skull with I^1–C/ br. and P^1–dP^2–M^3(germ)	(M)	72218
MANDIBLE		
Partial mandible with P_1–P_4 rt. and M_1–M_3	(M)	72219

FROM E. OF SADDLE HORSE PASS,[1] PENNINGTON COUNTY, SOUTH DAKOTA:

SKULL		
Skull with I^1–I^3 alv. and C/–M^3	(W)	45099

The field data of the above specimen state, "lower part of Middle *Oreodon* beds." (See discussion, p. 26.)

H. FROM SLIM BUTTE-BATTLE MOUNTAIN AREA, HARDING COUNTY, SOUTH DAKOTA

FROM 1 MI. N. OF SLIM BUTTE:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS (IMMATURE)		F:A.M.
Partial skull with I^2–dP^1–dP^4(germ), mandible (attached) with I_1–dP_2 (P_1 alv.), partial scapula, partial humerus, partial femur, partial tibia, and vertebrae	(I)	72049
3 SKULLS AND MANDIBULAR RAMI		
Partial skull with P^1–M^1 br. and M^2–M^3(br.) and partial mandible with I_1–P_3 rt. and P_4–M_2	(W‡)	49689

[1] Saddle Horse Pass is in the divide area between White River and Cheyenne River drainages.

		F:A.M.
The above superior premolars, although damaged, show decided crowding.		
Partial skull with I^1–dP^2–M^1 and mandible with I_1–I_2 rt. and I_3–dP_2–M_2(germ)	(I)	49773
Partial skull with C/(rt.)–dP^2–M^3(erupt.) and partial left ramus with I_1–P_3 rt. and dP_4–M_3(erupt.) (M_2 br.)	(I)	72050

SKULL

Inferior, anterior portion of skull with C/(br.)–dP^2–M^2	(I)	72052

MANDIBLE, IMMATURE

Partial mandible with I_1–dP_2 rt. and dP_3–M_3(germ)	(I)	49695

FROM HEAD OF POINT CREEK:

2 SKULLS

Partial skull with C/(rt.)–dP^2–M^3(germ)	(I)	49691
Skull with C/(br.)–dP^2–M^3(erupt.)	(I)	49693

FROM REVA GAP AREA:

SKULL

Cranium and M^2–M^3	(W+)	72051

MANDIBULAR RAMUS

Partial left ramus with I_1–P_1 rt. and P_2–M_3(br.)	(W‡)	49694

I. FROM 7 MILES SOUTH OF SOUTH HEART, STARK COUNTY, NORTH DAKOTA

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with I^3–M^3, partial mandible with /C–M_3, partial femur, 2 partial tibiae, 2 astragali, 2 calcanea, 2 partial pedes, vertebrae and ribs. Figure 23 (in part)	(W‡)	45468A
Partial left maxilla with dP^4–M^1, partial mandible with dP_4–M_2, partial radius, partial ulna, and calcaneum	(I)	45468B
The above 2 individuals were found associated in the field.		

MANDIBLE

Partial mandible with I_1–/C rt. and P_1(br.)–M_3 (P_4 br.)	(M)	72053

1a. **Otionohyus wardi degrooti**,[1] new subspecies

From "Zone C" of the Chadron Formation, Converse County, Wyoming; referred remains from Niobrara County, Wyoming; Dawes County, Nebraska; and Fall River County, South Dakota

DESCRIPTION

SKULL: Small size, equal to smaller examples of *O. wardi;* muzzle narrower on average than those of *O. wardi.* (See generic characters.)

MANDIBLE: Similar to those of *O. wardi;* same size comparisons as skull. (See generic description.)

DENTITION: Series smaller, especially premolar series; tendency to be lighter. (See generic description.)

LIMBS: Approximately equal to examples of *O. wardi.*

MEASUREMENTS: Tables 4 and 7 (pp. 104 and 146).

ILLUSTRATIONS: Figures 10, 11, 19–23, 52.

DISCUSSION

The remains of *Otionohyus wardi degrooti* provide additional evidence that forms from "Zone C" of the Chadron do not differ greatly from the related species occurring in "Zone A" of the Brule. The characters of *O. wardi* and *O. w. degrooti* are very similar. The examples of *Merycoidodon culbertsonii* from "Zone A" of the Brule and *M. c. browni* from "Zone C" of the Chadron also demonstrate only slight differences. Perhaps the division between the

[1] Named in honor of Mr. Everett DeGroot, a member of the Frick Laboratory field parties in Wyoming during the 1930's.

Chadron and Brule could be more logically drawn, both faunally and lithologically, between Brule faunal zones "A" and "B." (See discussion, p. 401.)

The holotype of *O. w. degrooti* is perhaps a female example, and the referred, F:A.M. 49723, a male. The type is decidedly of lighter construction, less width, and with lighter dentition than is noted in the referred skull. Although sex variation is suggested in this subspecies, the same variation is not apparent in examples of *O. wardi.*

The referred specimen from Wyoming was collected by Charles H. Falkenbach and associates, 1948; the Nebraska and South Dakota specimens, by Morris F. Skinner and associates, 1953.

Five specimens are here recorded:

HOLOTYPE

Skull with I^2–M^3, mandible with I_1–M_3, 2 partial humeri, 2 radii, 2 ulnae (1 partial), 2 partial manus, femur, 2 tibiae, astragalus, calcaneum, partial pes, vertebrae, and pelvis. (w+) Female example.	F:A.M. 49760	From "Zone C" of Chadron Formation, 30′ below "Purple White Layer," 8 mi. S.E. of Douglas, North Platte River drainage, Converse County, Wyoming; collected by Morris F. Skinner, Charles H. Falkenbach, and associates (Alan L. Lamb, Charles F. Falkenbach, Morris F. Skinner, Jr.), 1953 Figures 10, 11, 19–23, 52

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; (B) DAWES COUNTY, NEBRASKA; AND (C) FALL RIVER COUNTY, SOUTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, NORTHEAST OF INDIAN CREEK, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

SKULL		F:A.M.
Partial skull with I^1–M^3	(w‡)	49723

B. FROM WHITE RIVER DRAINAGE, ¼ MILE SOUTHWEST OF BRECHT STOCK DAM (=U.N.S.M. COLL. LOC. DW–104), DAWES COUNTY, NEBRASKA

2 MANDIBULAR RAMI		F:A.M.
Partial right ramus with P_2(rt.)–P_3	(M+)	72296
The above number includes two fragmentary rami with roots.		
Partial left ramus with P_3–M_2 and M_3	(w‡)	72312

C. FROM FLAT TOP BUTTE, HARRISON RANCH, FALL RIVER COUNTY, SOUTH DAKOTA

MANDIBULAR RAMUS		F:A.M.
Partial right ramus with P_1–P_2 rt. and P_3–M_3 (P_4 rt.)	(w)	72297
The above ramus is in three pieces. Although there are no actual contacts between the pieces, they appear to belong to one individual.		

3. **?Otionohyus vanderpooli,**[1] new species

From "Zone C" of the Chadron Formation, Sioux County, Nebraska

DESCRIPTION

SKULL: Small in size, slightly larger than examples of *O. wardi degrooti* and those of *Merycoidodon culbertsonii browni* (all from "Zone C" of Chadron), approximate size of examples of *O. wardi* (from "Zone A" of Brule); brain case slightly elongated; nasals moderately broad, posterior border acute; orbit small; malar shallow below orbit; lacrimal fossa large, deeper than in other examples of the Merycoidodontinae; posterior palatal projection extending to a point opposite last lobe of M^3.

MANDIBLE: (Unknown).

DENTITION: I^3 considerably larger than I^1

[1] Named in honor of Eugene Vanderpool, who was a member of the University of Nebraska State Museum field parties from 1930 to 1934.

and I^2; superior premolars more crowded and larger than in examples of *O. wardi degrooti*, more like larger examples of *O. wardi;* P^1–P^2 each with a weak anterior intermediate crest.

LIMBS: Within size range of examples of *O. wardi* and *O. w. degrooti*, smaller than those of *M. c. browni.*

MEASUREMENTS: Tables 4 and 7 (pp. 104 and 146).

ILLUSTRATIONS: Figures 10, 19, 22.

DISCUSSION

The holotype of *?Otionohyus vanderpooli*, the only known example of this new species, is questionably referred to this genus because the skull characters are midway between those of *Otionohyus* and those of *Merycoidodon*. The skull is narrower and the brain case is more elongated than that of *Otionohyus*, yet the skull is low and flat, and similar to examples of the genus *?Otionohyus*. The long and narrow skull is more like that of *Merycoidodon*. The more massive and more crowded premolars, and the exceptionally deep lacrimal fossa, differ from these elements in both *Otionohyus* and *Merycoidodon*.

One specimen is here recorded:

HOLOTYPE

Skull with I^1–M^3, humerus, partial femur, partial tibia, and fragments. (M+)	F:A.M. 49766	From "Zone C" of Chadron Formation, 8′ below base of Orella, Albert Meng Ranch area,[1] Cheyenne River drainage, Sioux County, Nebraska; collected by Ove Kaisen, Morris F. Skinner, and Morris F. Skinner, Jr., 1944 Figures 10, 19, 22

IIIA. OTIONOHYUS (OTAROHYUS), NEW SUBGENUS

SUBGENOTYPE: *Otionohyus (Otarohyus) bullatus* (Leidy).

DESCRIPTION

SKULL: Small in size; basal lengths ranging from 163 to 205 mm., widths from 86 to 132 mm.; mesocephalic; supraoccipital wings well extended posteriorly beyond occipital condyles; characters similar to those of *Otionohyus* except skull slightly higher, sagittal crest slightly higher, well-inflated bulla with hyoidal groove of varying depth, postglenoid process more massive, and lacrimal fossa as deep but not large.

MANDIBLE: Same characters as those of *Otionohyus* except for more robust ramus (deeper in examples from the upper stratigraphic sequence).

DENTITION: Same characters as genus; series remains light but with a tendency to become heavier in higher geologic sequence.

LIMBS: Short and light; slightly longer and more robust than examples of *Otionohyus*.

[1] From U.N.S.M. Coll. Loc. SX-13, 11 mi. W. and 11 mi. N. of Crawford.

MEASUREMENTS: Tables 4, 5, and 7 (pp. 104, 117, and 146).

ILLUSTRATIONS: Figures 11–13, 52 (skulls, mandibles, and dentitions), 19–23 (limbs).

DISCUSSION

The bullae of *Otionohyus* are minute in contrast to the well-inflated bullae of *O. (Otarohyus)*. The variation in the depth of the hyoidal grooves is not considered to be of generic significance. Although the bullae are larger in species that are recorded from higher geologic deposits, they are not so large as examples of *Merycoidodon (Anomerycoidodon)*, *M. (Blickohyus)*, *Paramerycoidodon (Barbourochoerus)*, and *P. (Gregoryochoerus)* from comparable faunal zones of the Brule.

The proposed sequence of the species of *Otionohyus (Otarohyus)* is as follows: *O. (O.) bullatus* from "Zone B" of the Brule; *O. (O.) cedrensis* from "Zone B" of the Brule, perhaps a side line of the phylum; *O. (O.) hybridus* from "Zone C" of the Brule; and *O. (O.) alexi* from "Zone D" of the Brule.

DISTRIBUTION

Four species and one subspecies of *Otionohyus (Otarohyus)* are known from the upper Oligocene (oreodont faunal zones "B," "C,"

TABLE 5

Otionohyus (*Otarohyus*), New Subgenus, and *Genetochoerus*, New Genus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*O.* (*O.*) *hybridus* (Leidy) Holotype A.N.S.P. 10860	*O.* (*O.*) *hybridus* (Leidy) Referred F:A.M. 72009	*O.* (*O.*) *hybridus helenae* (Douglass) Holotype C.M. 765	*O.* (*O.*) *alexi*, new species Holotype F:A.M. 72060	*G. periculorum* (Cope) Holotype A.M. 6397
Stage of wear of teeth	(w‡+)	(w+)	(I)	(M+)	(M+)
Length (incl. supraoccipital crest and incisors)	—	205.5	((190))	—	((185))
Basal length (from anterior notch of foramen magnum to posterior base of I^1	—	(177)	((173))	(190)	159
Width (max.)	—	120.5	((115))	125	((93))
Width of brain case (max.)	—	60	55	56	49.5
Width, interorbital (min.)	64.5	52.5	51	52	47.5
Distance from anterior rim of orbit to anterior base of C/.	—	76.5	—	83.5	67
Distance from anterior rim of orbit to supraoccipital crest	—	138.5	—	(130)	((120))
Length of nasals	—	—	—	(72)	—
Width of muzzle at infraorbital foramina	56	48.5	52.5	51.5	42.5
Width across canines	—	32	—	(44)	31.5
Length, C/–M^3 incl.	—	97	((93))	104	86
Length, P^1–M^3 incl.	(83.5)	82.5	((85))	90	76
Length, P^1–P^4 incl.	(44.5)	39.5	48	42.5	38.5
Length, M^1–M^3 incl.	(41.5)	45	41	48.5	39.5
Width of M^3 (max.)	(19.5)	16.5	19	19	15
Depth of malar below orbit	21	16	17	15	13.5
MANDIBULAR RAMUS				Referred F:A.M. 72065	
Stage of wear of teeth				(w‡)	
Length (max., incl. incisors)	—	160.5	—	—	145
Length, /C–condyle incl.	—	148	—	—	132.5
Depth of jaw under coronoid	—	(83)	—	—	69
Depth of jaw below anterior edge of M_3	—	35	35.5	41	29.5
Length, /C–M_3 incl.	—	101.5	—	—	91.5
Length, P_1–M_3 incl.	—	91.5	—	(98)	84
Length, P_1–P_4 incl.	—	43	—	(43.5)	38.5
Length, M_1–M_3 incl.	—	49	51.5	54.5	45.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

and "D" of the Brule) of Nebraska, South Dakota, North Dakota, and Montana. (See geologic distribution chart, p. 22.)

Summary of Species and Types

Four species and a subspecies of *Otionohyus* (*Otarohyus*) from 12 Brule (oreodont faunal zones "B" through "D") localities are here recorded:

1. *Otionohyus (Otarohyus) bullatus* (Leidy), from South Dakota; referred remains from Shannon, Pennington, Jackson, and Fall River counties, South Dakota; Sioux County, Nebraska; and Stark County, North Dakota. ("Zone B" of Brule.)

HOLOTYPE: Partial skull, A.N.S.P. 10681.

2. *Otionohyus (Otarohyus) cedrensis* (Matthew), from Logan County, Colorado; referred remains from Weld County, Colorado. ("Zone B" of Brule.)

HOLOTYPE: Skull, mandible, and skeletal elements, A.M. 8949. Figures 11–13, 20, 23.

3. *Otionohyus (Otarohyus) hybridus* (Leidy), from South Dakota; referred remains from Washabaugh and Jackson counties, South Dakota; and Sheridan County, Nebraska. ("Zone C" of Brule.)

HOLOTYPE: Partial skull, A.N.S.P. 10860.

3a. *Otionohyus (Otarohyus) hybridus helenae* (Douglass), from Broadwater County, Montana. (?"Zone C" of Brule.)

HOLOTYPE: Skull and mandible, C.M. 765. Figures 11–13.

4. *Otionohyus (Otarohyus) alexi*, new species, from Washabaugh County, South Dakota; referred remains from Washabaugh, Jackson, Shannon, Pennington, and Harding counties, South Dakota; Sioux County, Nebraska; and tentatively referred from Jackson County, South Dakota; and Colorado. ("Zone D" of Brule.)

HOLOTYPE: Skull, F:A.M. 72060. Figures 12, 13, 52.

1. **Otionohyus (Otarohyus) bullatus** (Leidy)

From oreodont faunal "Zone B" of the Brule Formation, South Dakota; referred remains from Shannon, Pennington, Jackson, and Fall River counties, South Dakota; Sioux County, Nebraska; and Stark County, North Dakota

Oreodon bullatus LEIDY, 1869, p. 106. SCOTT, 1890b, pl. 13, fig. 6 (not type). OSBORN AND WORTMAN, 1894, p. 218, fig. 5c (not type).

Eporeodon bullatus (Leidy): MARSH, 1875, p. 250. THORPE, 1937, p. 65 (figs. 28–30 not this species).

Oreodon (Eporeodon) bullatus (Leidy): SINCLAIR, 1924, p. 128.

Eucrotaphus jacksoni Leidy, in part: TROUESSART, 1898, p. 836.

Eucrotaphus jacksoni jacksoni (Leidy), in part: COPE, 1884a, p. 518.

Oreodon jacksoni (Leidy), in part: ROGER, 1896, p. 213.

Merycoidodon bullatus (Leidy): HAY, 1902, p. 665.

Merycoidodon bullatum (Leidy): STROMER, 1912, p. 199, fig. 183 (fig. not type).

Oreodon (Merycoidodon) bullatus (Leidy): O'HARRA, 1920, p. 150.

CHARACTERS

SKULL: Approximate size of examples of *Otionohyus wardi*, slightly smaller than those of *O. (O.) hybridus;* lacrimal fossa larger and deeper than last-mentioned species; bulla inflated, decidedly more inflated than minute ones of *O. wardi*, slightly less elongated (vertically) and with more prominent hyoidal groove than examples of *O. (O.) hybridus*. (See subgeneric description.)

MANDIBLE: Similar to examples of *O. wardi* and *O. (O.) hybridus;* lighter and shallower than those of *O. (O.) alexi*. (See subgeneric description.)

DENTITION: Similar to examples of *O. wardi*; premolars average lighter than those of *O. (O.) hybridus*, lighter than examples of *O. (O.) alexi*; P^1–P^3 each with short but noticeable anterior intermediate crest. (See subgeneric description.)

LIMBS: More massive and longer than examples of *O. wardi*.

MEASUREMENTS: Tables 4 and 7 (pp. 104 and 146).

ILLUSTRATIONS: Figures 11–13, 19–23, 52.

DISCUSSION

"Oreodon" bullatus was named by Leidy in 1869, and since that time the species has been referred to various genera (*Eporeodon, Eucrotaphus,* and *Merycoidodon*). The confusion, no doubt, was due to the lack of material from the various Brule faunal zones and the lack of stratigraphic field data.

Cope[1] considered the species *bullatus* as a synonym of *"Eucrotaphus jacksoni"* and *"E. jacksoni jacksoni"* and reported: "The typical specimen of the *Oreodon bullatus* Leidy agrees

[1] 1884a, pp. 517, 518.

so nearly with the original type of *Eucrotaphus jacksoni*, that I cannot doubt their pertinence to the same species. There are two specimens in the collection of the Philadelphia Academy, besides the last named, and at least one in the museum at Princeton. A specimen from the John Day, Oregon, cannot be distinguished from these. It agrees with Marsh's measurements and description of his *Oreodon occidentalis* [*Eporeodon occidentalis*, genotypic species] and no doubt represents it. Its identity with his *O. bullatus* has already been surmised by Leidy (Report U.S. Geol. Survey Terrs., I, p. 318)."

Leidy's statement was: "Professor Marsh has recently described some remains from the Miocene of Oregon, under the name of *Oreodon occidentalis* . . . He observes that it resembles *O. culbertsonii* in most of its cranial characters, but differs materially in the large auditory bullae. From this, I suspect the remains, together with those I have described from Oregon under the last-mentioned name, belong to the species I have elsewhere named *O. bullatus*." Leidy[1] originally described *bullatus* as a species of *Oreodon*. The early confusion of the usage of *Oreodon* was due to Leidy's preference for the name *Oreodon* to *Merycoidodon*. (See discussion under *Merycoidodon*, p. 33). Marsh[2] and Thorpe[3] placed *bullatus* under *Eporeodon*. Thorpe also tentatively referred three John Day specimens to *E. bullatus*. Later he[4] considered two of these specimens as plesiotypes of *E. bullatus*, and it is apparent that some of his specific characters were based on his John Day examples, as follows: "This species [*bullatus*] holds an intermediate position between *M. culbertsonii* and the upper Oligocene species of *Eporeodon*. It is, however, seemingly present in the upper Oligocene of the John Day Basin, as the specimens in the Marsh Collection show, but it has changed somewhat from the type species . . . while three skulls . . . are from the John Day Basin. . . . These three are all more robust than the type, with greater bizygomatic diameter and apparently a higher skull index." Two of these skulls here in question have been referred to *Eporeodon* (*Paraeporeodon*) *pacificus* (Cope) (Y.P.M. 10146 and 12299). The latter was figured by Thorpe (figs. 28–30) as the species *bullatus*. The genus *Eporeodon* and the age of the John Day deposits are discussed on page 199. Thorpe[5] also referred a Colorado skull to this species, Y.P.M. 12284.

Cope's suggestion that the species *bullatus* be considered a synonym of "*Eucrotaphus jacksoni*" is not here considered valid, nor was it accepted by other authors reporting on the oreodonts. The bulla of *Otionohyus* (*Otarohyus*) *bullatus* is decidedly more inflated than that of "*E. jacksoni*."

Leidy's conclusion that *Eporeodon occidentalis* was a synonym of *O.* (*O.*) *bullatus* also has not been accepted. The bulla of the former is decidedly more conical than that of the latter. There are other character differences which are discussed under *Eporeodon occidentalis* (p. 201).

Trouessart[6] referred the species *bullatus* to "*Eucrotaphus*" (see discussion of "*Eucrotaphus*," p. 165). Both Cope[7] and Roger[8] considered the species *bullatus* as a synonym of "*Eucrotaphus jacksoni*." The latter, a questionable form, has a well-inflated bulla which is more rounded and lacks the typical hyoidal groove; also the postglenoid process is much more massive. (See discussion, p. 165 and fig. 11.)

Sinclair[9] recorded five specimens of *O.* (*O.*) *bullatus*, two from the "Lower Nodular Zone," one from "30 feet above lower zone of rusty nodules," and two from "Upper Nodular Zone." No specimen numbers were indicated and it was not stated how complete the individuals were, i.e., if the bullae were present on those from the "Lower Nodular Zone." Without the bulla of a specimen available it would be very difficult to separate accurately the examples of various forms that occur in the Brule sequence. Those examples from "Zone A" of the Brule no doubt had small (minute) bullae as are found in other examples from that zone.

Sinclair further stated: "There is, however, never the slightest danger of confusing *Oreo-*

[1] 1869, pp. 92, 106, 380.
[2] 1875, p. 250.
[3] 1921c, p. 104.
[4] 1937, p. 66.
[5] 1924b, 220; 1937, p. 67.
[6] 1898, p. 836.
[7] 1884a, p. 517.
[8] 1896, p. 213.
[9] 1924, p. 102.

CHART 5 (THIS PAGE AND OPPOSITE PAGE)

Otionohyus (*Otarohyus*) *bullatus* (LEIDY). COMPARATIVE MEASUREMENTS[a] OF 11 ASSOCIATED INDIVIDUALS

	F:A.M. 45176B		F:A.M. 45176A		F:A.M. 45176E		F:A.M. 45176D		F:A.M.
	Left	Right	Left	Right	Left	Right	Left	Right	Left
M^3 [c]	11.5	—	(11.2)	11.2	11.1	10.5	10.4	11	—
$C/-M^3$, L [d]	97.2	—	—	96.4	—	—	—	—	—
P^1-M^3, L	83.8	—	—	82.2	78.7	77.5	84.3	85.5	—
P^1-P^4, L	43	—	—	40	38.9	38.2	42.7	42.7	—
M^1-M^3, L	43.2	—	44	45.1	42.3	(41.4)	45.4	44.5	—
P^1, L	9	—	—	9.3	9.5	9.4	9.3	9.5	9.2
P^1, W [e]	6.5	—	—	6	6.7	6.8	6.4	6.3	6
P^2, L	9.5	—	10.8	10.7	10.7	10.3	10.8	11	—
P^2, W	9	—	8.6	8.2	8.6	8.5	7.7	8	—
P^3, L	11	—	10.6	11.6	10.5	10.5	11.4	11	—
P^3, W	11	—	10.4	10.2	9.9	9.8	10.5	10.5	—
P^4, L	10.2	—	10.4	9.4	9.5	9.8	9.4	10.3	—
P^4, W	14	—	12.8	14.3	12.7	12.9	13.3	14	—
M^1, L	12.8	—	14.1	14.2	13.7	(12.9)	13.6	13.5	—
M^1, W	15.4	—	14.4	15	14.5	14.4	15.6	16	—
M^2, L	16.5	—	15.8	16.1	16.5	16.5	16.5	16.9	—
M^2, W	18.2	—	15.8	17.1	17	16.8	18	18	—
M^3, L	16.7	—	(16)	17	17.4	17.3	18.4	18.6	—
M^3, W	18.5	—	17	17.4	16.2	16.7	17.4	18.2	—
Malar depth below orbit	16.2	—	—	15.2	12.2	13	16.6	15.7	—
Ramus, depth below M_3 [f]	33.7	32.4	30	29.7	—	29.7	29.3	29.5	—
$/C-M_3$, L	96.5	—	100.8	96.3	(90.5)	89.5	101.5	98.5	—
P_1-M_3, L	89	—	92.5	89.8	85.2	83.8	94.5	(91.4)	—
P_1-P_4, L	42.5	—	45	42.3	36.4	36.7	43.7	40.5	—
M_1-M_3, L	47.5	(46.1)	48.2	47.5	48.9	47.2	51.4	50.7	—
P_1, L	10.5	—	12	11.1	10.3	10.5	9.7	—	—
P_1, W	7.3	—	6.5	6.5	6.4	6.8	6.9	—	—
P_2, L	9.2	9	10.2	10.2	9.7	10	10	(9.5)	—
P_2, W	5.6	5.2	5.5	5.3	5.3	5.2	5.6	—	—
P_3, L	11.7	10	11.6	11.6	10.6	10.5	11.6	11.9	—
P_3, W	7.5	7.5	6.2	6.4	6.8	7.2	6.9	7.6	—
P_4, L	11.7	11.7	12.2	12.5	11	11	11.9	11.8	—
P_4, W	10	9.6	8.9	9.2	9.5	8.7	8.5	9	—
M_1, L	12	(12.1)	12.8	13.4	12.7	13	13	13	—
M_1, W	10.5	10.5	10.9	10.7	10.3	10.8	11.1	11.2	—
M_2, L	14.5	14.3	14.5	14.5	14	14.1	14.5	15	—
M_2, W	12.6	12	12.5	12.3	11.5	12	12.3	12.9	—
M_3, L	21.3	21.2	21.4	21.5	21.5	21.2	23.2	22.4	—
M_3, W	13	12.6	11.9	12	11.7	11.3	12.5	12.6	—

[a] ( ), Approximate. All measurements in millimeters.

[b] Degree of variation based on the larger measurement.

[c] Height of external enamel.

CHART 5

45176F Right	F:A.M. Left	45176C Right	F:A.M. Left	45176G Right	F:A.M. 45176H Left	F:A.M. 45176I Right	F:A.M. 45176J Left	F:A.M. Left	45176K Right	Per Cent of Differ-ence[b]
10.5	10	10	10	—	—	—	—	—	—	13+
(91.5)	—	—	—	—	—	—	—	—	—	6−
(81.3)	(85)	86.1	—	—	—	—	—	—	—	10−
(41.7)	(41)	43.7	—	37.8	—	—	—	—	—	13+
42.3	45.7	44.7	—	—	—	—	—	—	—	9+
—	—	(10)	—	9	9.1	—	—	—	—	10
—	—	—	—	6.7	6.7	—	—	—	—	1+
10	(10.5)	11.2	—	10.2	10.4	—	—	—	—	15
8.2	—	8.6	—	7.8	7.7	—	—	—	—	14+
11	11.9	11.9	—	(10.5)	—	—	—	—	—	11+
11	11	10.7	—	9	—	—	—	—	—	18
10.6	9.5	9.8	—	9.1	—	—	—	—	—	14+
14	12.2	13.7	—	—	—	—	—	—	—	14+
13.2	13.5	13.6	—	—	—	—	13.9	—	—	9+
—	16.4	16.2	—	—	—	—	14.4	—	—	12+
16.5	(16.1)	16.1	16.3	—	—	—	—	—	—	6+
(17.7)	(18.1)	18.1	17	—	—	—	—	—	—	13+
17.5	18.5	18.7	16.7	—	—	17	—	—	—	14+
—	19.4	19.2	16.6	—	—	(16)	—	—	—	17+
—	17.8	17.7	—	—	—	—	—	—	—	26+
—	—	36.6	—	—	—	—	—	—	29.4	19+
—	—	—	—	—	—	—	—	90	—	11+
—	—	93.3	—	—	—	—	—	84.5	—	11+
—	41.6	41	—	—	—	—	—	40.4	38.1	12+
—	—	42.8	—	—	—	—	—	44.5	—	4−
—	(9.3)	—	—	—	—	—	—	9.9	—	10−
—	—	—	—	—	—	—	—	6.5	6.6	12+
—	10.3	11.3	—	—	—	—	—	9.7	9.4	20+
—	—	—	—	—	—	—	—	6	5.5	13+
—	12	—	—	—	—	—	—	11.3	11.8	16+
—	8	—	—	—	—	—	—	7.3	7.2	22+
—	13.1	12.2	—	—	—	—	—	10.7	10.6	19+
—	9.9	—	—	—	—	—	—	8.9	9.1	15
—	—	13.1	—	—	—	—	—	13.1	12.3	8+
—	—	11.5	—	—	—	—	—	10.2	10.3	11+
—	—	16.3	—	—	—	—	—	(13)	14.2	20+
—	—	13.5	—	—	—	—	—	12	11.5	14+
—	—	23.4	—	—	—	—	—	(21.5)	—	9+
	—	12.9	—	—	—	—	—	11.1	—	14+

[d] L, greatest anteroposterior length.
[e] W, greatest width.
[f] Measurement taken just anterior to M_3.

don culbertsoni culbertsoni with *Eporeodon bullatus* if the auditory region has been preserved. Quite unexpected data regarding the stratigraphic range of the latter are afforded by our collections of the past three years. From the presence of eporeodons (*E. major*) with greatly distended bullae in the *Protoceras* beds, and of forms with small rugged bullae in the *Oreodon* beds, with a single example of 'the transitional form *O. bullatus*' from beds of intermediate position, Osborn and Wortman were led to suggest[42] [Osborn and Wortman, 1894, p. 219.] that the range in time corresponds with the evolution of the bullae. This, however, is not the case, for typical *Eporeodon bullatus*, agreeing absolutely with Fig. 5C of Osborn and Wortman's paper, occurs in both noduliferous horizons of the *Oreodon* beds and probably in the *Protoceras-Leptauchenia* beds as well. The type of *Oreodon* (*Eporeodon*) *bullatus* is from the *Titanotherium* beds[13] [Leidy, 1869, pp. 104–105], and the species is tentatively identified by Thorpe[14] [1921c, p. 104] from the John Day, certainly the greatest vertical range of any White River form." Leidy did note that the holotypes of *"Oreodon" affinis* [=*Miniochoerus affinis* from "Zone A" of the Brule], *"O." hybridus* [=*Otionohyus* (*Otarohyus*) *hybridus* from "Zone C" of the Brule], and *"O." bullatus* [=*O.* (*O.*) *bullatus* from "Zone B" of the Brule] all occurred in "the lowest bed of the tertiary deposits of the Mauvaises Terres of the White River, or bed A of his [Hayden's] table, as indicated on page 20."

In these particular instances, and throughout this revision, the geologic occurrences of many of the holotypes were verified as nearly as possible by the writers. These conclusions are based on referred specimens that are similar to the types and do bear geologic evidence. Many of the early oreodont holotypes lack geologic documentation. The evidence would indicate that, in this particular instance, Hayden's "bed A" includes at least three different faunal zones. As stated elsewhere, titanothere remains are not restricted to the Chadron deposits but are also found in oreodont faunal "Zone A" of the Brule.

Osborn and Wortman's conclusion that the "range in time corresponds with the evolution of the bullae" is here considered to be correct for the oreodonts except for the Miniochoerinae, in which the auditory bullae remain small (minute), and the Leptaucheniinae, in which the bullae are well inflated throughout their known geologic occurrence.

Further evidence that "the range in time corresponds with the evolution of the bullae" was suggested by Osborn and Wortman (p. 218) in their statement: "There is a single skull of this species [*bullatus*] in our collection (No. 611) which was obtained from the second 'nodular layer,' from seventy-five to one hundred feet above the 'red layer' of the 'Oreodon Bed.' It is a matter of much interest to note that the bullae are much more inflated than in either *O.* [*Merycoidodon*] *culbertsonii* or *O.* [*Miniochoerus* (*Paraminiochoerus*)] *gracilis*."

Sinclair also noted that Thorpe[1] "tentatively identified" the species *bullatus* from "the John Day." Thorpe's conclusions are discussed in this report on page 119. The age of the John Day deposits is considered on page 199.

Examples of *O.* (*O.*) *bullatus* differ noticeably from those of *O. wardi* ("Zone A") in having an inflated bulla, whereas the latter has a minute one. The bulla sequence is as follows: small in "Zone A" of the Brule, inflated and prominent hyoidal groove in "Zone B," and more rounded and less grooved, respectively, in zones "C" and "D." This sequence is typical of all phylogenetic lines in the Merycoidodontinae. It is here considered that *O.* (*O.*) *bullatus* developed from *O. wardi*, and in turn gave rise to *O.* (*O.*) *hybridus*.

The F:A.M. specimens here recorded were collected by Ralph Mefferd, Morris Skinner, and party, 1938–1940, 1944, 1945, 1950, and 1951. The U.N.S.M. material was collected by T. M. Stout and associates, 1937.

Sixty-five specimens are here recorded:

[1] 1921c, p. 104.

HOLOTYPE

Partial skull with C/(rt.)–M^3 (P^1 br.).	A.N.S.P. 10681 (w)	From oreodont faunal "Zone B" of Brule Formation,[1] Mauvaises Terres, South Dakota; collected by Joseph Jeanes, 1866

REFERRED FROM (A) SHANNON, (B) PENNINGTON, (C) JACKSON, AND (D) FALL RIVER COUNTIES, SOUTH DAKOTA; (E) SIOUX AND ?DAWES COUNTIES, NEBRASKA; AND (F) STARK COUNTY, NORTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1½ MI. W. OF S. END OF SHEEP MT.:

SKULL, IMMATURE — F:A.M.

Partial skull with P^1(erupt.)–dP^2–M^2(germ) (dP^2–dP^4 br.) . . . . (I) 72233

FROM 1½ MI. W. OF SHEEP MT.:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with C/(rt.)–M^3 (P^1 br.), mandible with P_1(rt.)–M_3, 2 partial humeri, 2 radii (1 partial), 2 partial ulnae, 2 partial manus, 2 partial femora, 2 tibiae, partial fibula, 2 astragali, 2 calcanea, 2 partial pedes, and vertebrae. Figures 20, 23 (in part) . . . . (w) 45268

FROM ½–1½ MI. N. OF COTTONWOOD PASS[2] (BIG CORRAL DRAW AREA):

SKULL AND MANDIBLE

Partial skull with C/(rt.)–M^3 and partial mandible with P_1(br.)–M_3 . . . . (M+) 72056

SKULL

Partial skull with C/(rt.)–M^3 . . . . (w) 45275

FROM W. BIG CORRAL DRAW:

2 SKULLS AND MANDIBLES

Partial skull with P^1–M^3 (P^2 br.) and partial mandible with P_2–M_3 . . . . (w) 45270

Partial skull with I^3–C/ br. P^1–M^3 and mandible with I_1–/C rt. and P_1–M_3 . . . (w+) 45271

FROM DIVIDE AREA BETWEEN BIG AND LITTLE CORRAL DRAWS:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with C/(rt.)–M^3 (P^1 br.), partial mandible with P_3–M_3, 2 partial scapulae, partial humerus, and partial radius . . . . (w‡‡) U.N.S.M. 28084

SKULL, IMMATURE

Partial skull with dP^3–M^3(germ) . . . . (I) 28138

FROM QUINN DRAW AREA (COLLECTED BY H. R. WANLESS, 1921):

SKULL AND MANDIBLE (ATTACHED) — P.U.

Partial skull with C/–M^3 and mandible with I_1–M_3 . . . . (?w) 12695[3]

FROM BATTLE CREEK DRAW (COLLECTED BY H. R. WANLESS, 1921):

SKULL AND MANDIBLE (ATTACHED)

Skull with I^1–M^3 and mandible with I_1–M_3 . . . . (?w) 12743

[1] The present writers assume that the holotype is from "Zone B" of the Brule Formation, since the referable material, which has associated geologic data, is from that faunal zone.

[2] Cottonwood Pass is in the divide area between the Cheyenne River and White River drainages.

[3] Sinclair (1924) also referred a skull, P.U. 12691, to this species, from "upper zone of Rusty Nodules, Lower *Oreodon* beds." The present writers have not examined this specimen. It is now in the paleontological collections of the University of California.

FROM BETWEEN BATTLE CREEK CANYON AND BATTLE CREEK DRAW:

SKULL, IMMATURE		F:A.M.
Partial skull with $C/$(br.)–dP^1–M^3(germ)	(I)	72283

A′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM S. END OF SHEEP MT.:

MAXILLAE AND MANDIBLE, IMMATURE		F:A.M.
Partial left and right maxillae with dP^2–M^2 and partial mandible with P_1–dP_2–M_2.	(I)	72232

FROM E. SIDE OF HARNEY SPRINGS RANGE, SE. OF SHEEP MT.:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with I^1–M^3, partial mandible with P_1(rt.)–M_3, 2 partial scapulae, 2 humeri (1 partial), 2 partial radii, partial ulna, 2 femora, 2 tibiae, astragalus, partial pes, partial pelvis, and vertebrae. Figures 11–13, 19, 21, 22, 52	(w+)	45267
11 ASSOCIATED INDIVIDUALS		
Partial skull with $C/$–M^3 and mandible with I_1–M_3	(w+)	45176A
Left anterior of skull with I^3(rt.)–M^3 and partial mandible with I_1(rt.)–M_3	(w+)	45176B
Partial skull with $C/$(rt.)–M^3 (P^1 br.) and partial mandible with P_1(rt.)–M_3	(w‡)	45176C
Inferior anterior portion of skull with $C/$(rt.)–M^3 and mandible with I_1–$/C$ br. and P_1–M_3	(w+)	45176D
Anterior portion of skull with I^1–$C/$ rt. and P^1–M^3 and mandible with I_1–I_3 rt. and $/C$(br.)–M_3	(w)	45176E
5 MAXILLAE		
Partial left and right maxillae with $C/$(rt.)–M^3 (M^1 and M^3 br.)	(w)	45176F
Partial left and right maxillae with I^1(rt.)–M^2 (I^3 and $C/$ rt.)	(w+)	45176G
Partial left maxilla with $C/$(br.)–P^2	(w)	45176H
Partial left maxilla with M^1–M^2(br.)	(w)	45176I
Partial left maxilla with P^4(br.)–M^1	(w+)	45165J
MANDIBLE		
Partial mandible with I_1–$/C$ br. and P_1–M_3	(w+)	45176K

It is possible that F:A.M. 45176H and K belong to the same individual.

SKELETAL ELEMENTS		
Humerus, partial radius, partial ulna, 2 partial manus, 2 femora, 2 tibiae, and vertebrae		45176A–B

The position in the field block of the above elements suggests the association of A and B numbers.

4 partial scapulae, 6 partial humeri, 5 partial radii, 2 partial ulnae, 5 partial femora, 5 partial tibiae, manus and pes elements, pelvic fragments, vertebrae, and skull fragments		45176A–K

See table 5 for comparison of measurements of above associated specimens.

FROM E. SIDE OF HARNEY SPRINGS RANGE: SPRING CREEK DRAINAGE:

5 SKULLS AND MANDIBLES		
Partial skull with $C/$(rt.)–M^3 and mandible with I_1–I_3 br. and $/C$–M_3 (P_1 br.)	(M+)	45269
Partial skull with $C/$(br.)–M^3(br.) (P^1 rt. and P^2 br.) and partial mandible with P_1–M_3 (P_2 br.)	(w)	45274
Partial skull with I^1(rt.)–M^3 (I^2 br.) and partial mandible with I_1(rt.)–M_3	(w‡‡)	45361
Anterior inferior portion of skull with $C/$–M^3 and partial mandible with P_2–M_3	(w‡)	45362
Partial skull with P^3–M^3 and partial mandible with P_1(rt.)–M_3 (P_2 br.)	(w+)	49787
SKULL		
Partial skull with $C/$(br.)–dP^2–M^3(erupt.)	(I)	49788

MAXILLAE, IMMATURE		F:A.M.
Partial left and right maxillae with dP^3–M^2(br.)	(I)	72225

FROM SE. OF PASS IN HARNEY SPRINGS RANGE:

SKULL		
Anterior portion of skull with C/–M^3(br.)	(W+)	45263

FROM ½ MI. S. OF HARNEY SPRINGS RANGE:

SKULL		
Partial skull with C/(rt.)–M^3 (P^1 rt. and P^2 br.)	(W)	45273

FROM HEAD OF SPRING CREEK, SE. OF SHEEP MT.:

SKULL		
Partial skull with I^2(alv.)–M^3 (I^3–C/ rt.)	(W‡$^+$)	45261

FROM 8 MI. N. OF ROCKYFORD:

MAXILLAE AND MANDIBLE		
Partial left and right maxillae with P^1–M^2(br.) and partial mandible with P_1(rt.)–M_3(br.)	(W+)	72111

FROM ¾ MI. E. OF CEDAR BLUFFS:

SKULL, IMMATURE		
Partial skull with C/(rt.)–dP^3(br.)–M^3 (P^2 germ)	(I)	45276

FROM 5 MI. NW. OF SLIM BUTTE:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Partial skull with C/–M^3, partial mandible with P_4–M_3, partial radius, partial manus, partial tibia, astragalus, and partial calcaneum	(W)	49792

2 SKULLS AND MANDIBLES		
Partial skull with C/(rt.)–M^3 and partial mandible (attached) with P_2–M_3	(M)	49790
Partial skull with C/–M^3 and mandible (attached) with I_1–M_3	(W)	49791

The above dentition shows a greater difference in ratio of molars to premolars (length of former greater) and greater depth to ramus below anterior border of M_3 than average examples.

2 SKULLS		
Partial skull with C/(rt.)–M^3 (P^1 br.)	(W‡)	49794
Partial skull with P^3–M^3	(M)	72147

The field data accompanying the above five specimens indicate that they were derived from "the Upper *Oreodon* beds" = oreodont faunal "Zone C" of Brule. However, the specimens are similar to examples from oreodont "Zone D."

B. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM MILLER BASIN, BETWEEN SCENIC AND IMLAY:

SKULL AND MANDIBLE		F:A.M.
Partial skull with P^2–M^3 and partial mandible with I_1–M_3 (P_1 br.)	(W‡)	45277

FROM IMLAY AREA:

SKULL, IMMATURE		
Skull with C/–M^3 (P^1 br., left P^2–P^4 erupt., right dP^3(br.)–dP^4)	(I)	49795

There seems to be an error in the data of the above specimen, as it is marked "Lower *Oreodon* beds." This may have been a talus specimen which had been derived from the overlying deposits.

C. FROM WHITE RIVER DRAINAGE, 1 MI. E. OF NORBECK PASS,[1] JACKSON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE		F:A.M.
Partial skull with P^1(br.)–M^3 and mandible with I_1(alv.)–M_3 (I_2–/C alv.)	(W+)	49797
SKULL		
Partial skull with P^1–P^3 rt. and P^4–M_3	(M)	49798

The above skull has larger dentition and bullae than usual for the species.

D. FROM WHITE RIVER DRAINAGE, 6 MILES SOUTHEAST OF OELRICHS, FALL RIVER COUNTY, SOUTH DAKOTA

SKULL, MANDIBULAR RAMUS, AND VERTEBRAE		F:A.M.
Partial skull with C/–M^3, partial left ramus with M_2–M_3(br.), and vertebrae	(W)	49796

FROM "WHITE RIVER," SOUTH DAKOTA,[2] 1892:

SKULL		A.M.
Skull with I^1(rt.)–M^3 and mandible with I_1(rt.)–M_3 (/C and P_1 br.)	(M+)	611

Figured by Osborn and Wortman, 1894, fig. 5c; Thorpe, 1937, fig. 7.

FROM SILAR RANCH, PASS CREEK (COLLECTED BY ALBERT THOMSON, 1904):

SKULL AND MANDIBLE (ATTACHED)		
Skull with I^2–M^3 and mandible with I_1–M_3	(W‡)	12321

The field data of the above specimens state "Lower Oreodon," but the bulla indicates "Zone B" (="Middle Oreodon") of the Brule. Perhaps this is a talus specimen.

E. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

SKULL, MANDIBLE (ATTACHED), AND SKELETAL ELEMENTS		F:A.M.
Skull with I^1–I^3 rt. and C/–M^3, mandible with /C–M_3, 2 partial humeri, partial radius, partial ulna, partial tibia, partial astragalus, and calcaneum	(W)	72005
SKULL AND MANDIBLE (ATTACHED)		
Skull with C/(rt.)–M^3 and mandible with P_2–M_3	(M+)	72006
2 SKULLS		
Partial skull with P^1–M^3	(W‡+)	72007
Skull with C/–M^3	(W+)	72008

F. FROM ?CROW BUTTE, DAWES COUNTY, NEBRASKA (COLLECTED BY J. Y. NELSON, OCTOBER 23, 1873)

SKULL		Y.P.M.
Partial skull with P^1–M^3	(W)	12447

Thorpe (1937, p. 70) recorded this specimen as coming from "Crow Buttes, South Dakota," but such a locality could not be located on a map by the writers. There is, however, a Crow Butte in Dawes County, Nebraska, just east of Fort Robinson. Elwyn L. Simons of the Y.P.M. (letter May 5, 1964) reported that "it is probably Crow Buttes, Nebraska." He also states that "In Catalogue Book, locality is given as Crow Buttes, Nebraska, in some cases and Crow Buttes, South Dakota, in others, though date of collection is the same." Thorpe provisionally referred this specimen to "*Eporeodon helenae.*" (See present report, p. 132.)

[1] Norbeck Pass is in the divide area between the White River and Bad River drainages.
[2] Exact locality unknown to present writers.

G. FROM STARK COUNTY, NORTH DAKOTA

FROM 7 MI. S. OF SOUTH HEART:

5 SKULLS AND MANDIBULAR RAMI

		F:A.M.
Partial skull with C/–P^1 rt. and P^2(br.)–M^3 (P^3–M^1 br.) and partial mandible with I_1–I_3 alv. and /C–M_3	(M)	49799
Partial skull with C/–P^3 br. and P^4–M^3 and partial right ramus (attached) with M_1(br.)–M_3	(W+)	49800
Skull with I^1–dP^2–M^3(germ) and mandible (attached) with I_1–dP_3–M_3(germ)	(I)	72000
Partial skull with P^1–dP^2–M^3(erupt.) (P^3 germ) and partial right ramus with I_2(alv.)–dP_4–M_2 (I_3 rt., /C alv. and P_1 rt.)	(I)	72001
Posterior portion of skull with (associated) P^3–M^3 and partial mandible with M_1–M_2 rt.	(M)	72002

MAXILLA

Partial right maxilla with P^4(rt.)–M^3	(W+)	49716

2 MANDIBULAR RAMI

Partial left ramus with P_3(rt.)–M_3 (M_2 br.)	(M+)	49719
Partial mandible with P_1(br.)–M_1 (P_2 rt. and P_3–P_4 erupt.)	(I)	72004

FROM LEO FITTERER RANCH, 13 MI. S. AND 8 MI. W. OF DICKINSON:

MANDIBULAR RAMUS

Partial left ramus with I_3(rt.)–M_3 (/C–P_1 alv.)	(W+)	72003

2. ?Otionohyus (Otarohyus) cedrensis (Matthew)

From ?faunal zone "Zone C" of the Brule Formation, Logan County, Colorado; tentatively referred remains from Logan and Weld counties, Colorado

Eporeodon major cedrenis MATTHEW, 1901, p. 396. THORPE, 1937, p. 75, pl. 5, figs. 4–6.

Eporeodon cedrensis (Matthew): HAY, 1930, p. 782.

CHARACTERS

SKULL: Small, within size range of smaller examples of *O.* (*O.*) *bullatus*; low; lacrimal fossa large and deep, comparable with examples of *O.* (*O.*) *bullatus*; bulla well inflated, with greater variation than in examples of *O.* (*O.*) *bullatus*; hyoidal groove prominent.

MANDIBLE: Shallow; ascending ramus low.[1] (Known only from immature holotype.)

DENTITION: Similar to more robust examples of *O.* (*O.*) *bullatus*; P^1–P^3 each with prominent anterior intermediate crest. (Inferior dentition known from immature holotype only.)

[1] The immature mandible of the holotype is the only known specimen. This individual would have had to grow considerably larger to have attained the same depth of ramus and ascending ramus as found in *O.* (*O.*) *bullatus*.

LIMBS: Short and light; comparable with examples of *Otionohyus wardi*. (Known only from immature holotype.)

MEASUREMENTS: Tables 4 and 7 (pp. 104 and 146).

ILLUSTRATIONS: Figures 11–13, 20, 23.

DISCUSSION

Matthew in his original description, stated, "A number of skulls and incomplete skeletons from horizon C are referable to this genus [*Eporeodon*] and may be placed provisionally as a dwarfed variety of *E. major* from South Dakota." No numbers were cited for the material in question, nor were the particular specimens again mentioned by Matthew or subsequent authors. The immaturity of the holotype of *cedrensis*, A.M. 8949, seems to eliminate the possibility that any of Matthew's additional specimens were complete enough for identification. These same specimens, however, might now be classified under a different genus and species.

Matthew further commented on the "general absence of the lacrimal pit." Thorpe[2] agreed with Matthew and wrote, "An unusual char-

[2] 1937, p. 75.

acter is the apparent absence of the lacrimal fossa, which may be due to adolescence." Additional preparation of the type specimen indicates that a prominent lacrimal fossa is present. This character is also evident in the referred specimens.

Loomis[1] referred the holotype of *cedrensis* to *"Eporeodon" relictus* (=*Paramerychyus relictus*[2]), apparently not realizing that A.M. 8949 was the number of the holotype of *cedrensis*. Thorpe[3] noted that the specimen was Matthew's holotype and stated, "Loomis was quite right in noting the resemblances between his holotype of *E.* [*P.*] *relictus* and Matthew's type of *E. m. cedrensis*." It should be noted that the former species comes from lower Miocene deposits (Harrison equivalent) and the latter from middle Oligocene sediments (lower Brule). Thorpe further reported that "the U-shaped palatonarial border [was] slightly back of the last molars." Actually the M^3's are germs and extend posteriorly beyond the palatonarial border.

The American Museum catalogue states that the holotype, A.M. 8949, came from "Castle Rock, Cedar Creek, Colorado, Horizon, White River." Matthew[4] stated that the holotype was from the "*Leptauchenia* beds." Thorpe gave the type locality as "Castle Rock, Logan County, northeastern Colorado" and the geologic horizon as "Upper Oligocene (Martin Canyon)."

The geologic occurrences of the holotype and the specimens herein tentatively referred are unknown. The various examples may have occurred in different faunal zones of the Brule. The holotype (skull), A.M. 8949, is of an immature individual and exhibits a bulla similar to what would be expected from "Zone B" of the Brule, but the dentition is more massive. The bullae of skull A.M. 8946A are more inflated than those of the holotype and example F:A.M. 45272, and suggest a stage of development that might be anticipated from "Zone C" of the Brule. All the examples are poorly preserved, thus making comparisons difficult. With the exception of the anterior portion of the skull, A.M. 8946B, which is badly crushed laterally, the other available skulls are compressed vertically; in fact they appear lower than those of *O.* (*O.*) *bullatus*. When a complete and mature skull of this species is available for comparison it may prove that *O.* (*O.*) *cedrensis* is equivalent to one of the other named species.

The F:A.M. referred specimens were collected by William Klaus and John C. Blick, 1931.

Six specimens are here recorded:

HOLOTYPE

Partial skull with I^1–dP^2–M^3 (germ), mandible with I_1–dP_2–M_3(germ), 2 partial scapulae, partial humerus, 2 radii, 2 ulnae, partial manus, partial pelvis, vertebrae, and fragments. (I)	A.M. 8949	From ?oreodont faunal "Zone B" of Brule Formation,[5] Castle Rock, Cedar Creek, Logan County, Colorado; collected by American Museum party, 1898 Figured by Thorpe, 1937, pl. 5, figs. 4–6 This report, figures 11–13, 20, 23

TENTATIVELY REFERRED FROM (A) LOGAN AND (B) WELD COUNTIES, COLORADO

A. FROM CASTLE ROCK, CEDAR CREEK, LOGAN COUNTY, COLORADO (COLLECTED BY H. T. MARTIN, 1898)

2 ?ASSOCIATED SKULLS		A.M.
Partial skull with C/–M^3	(w)	8946A
Anterior portion of skull with C/(br.)–M^3	(w)	8946B

[1] 1924b, p. 36.
[2] See Schultz and Falkenbach, 1947, p. 249.
[3] 1937, pp. 75, 76.
[4] 1901, pp. 368, 396.
[5] The exact faunal zones is not known. See discussion above.

B. FROM PAWNEE BUTTES AREA, WELD COUNTY, COLORADO (COLLECTED BY JOHN C. BLICK AND WILLIAM KLAUS, 1931)

3 SKULLS		F:A.M.
Partial skull with P^1–M^3 (P^2 br.). Figures 12–13	(w+)	45272
Partial skull with I^3–M^3(br.) (C/ absent, P^1–M^1 br.)	(w‡+)	72057
Anterior inferior portion of skull with P^1–M^3	(w‡+)	72058

3. **Otionohyus (Otarohyus) hybridus** (Leidy)

From oreodont faunal "Zone C" of the Brule Formation, South Dakota; referred remains from Washabaugh and Jackson counties, South Dakota; and Sheridan County, Nebraska

Oreodon hybridus Leidy, 1869, p. 105, pl. 9, fig. 4 (caption of fig. states *"O. major,"* description of pl., p. 457, reads "Variety of *O. major?*").

Merycoidodon hybridus (Leidy): Hay, 1902, 179, p. 666.

Merycoidodon (*Oreodon*) *hybridus* (Leidy): Cook, 1912, p. 35.

Oreodon (*Merycoidodon*) *hybridus* (Leidy): O'Harra, 1920, p. 150.

Eporeodon hybridus (Leidy): Thorpe, 1924b, p. 221.

Eporeodon major hybridus (Leidy): Thorpe, 1937, p. 77, fig. 38.

Characters

Skull: Intermediate in size between examples of *O.* (*O.*) *bullatus* ("Zone B" of the Brule) and those of *O.* (*O.*) *alexi* ("Zone D"); lacrimal fossa most shallow of subgenus; paroccipital process wider at base than in examples of *O.* (*O.*) *bullatus*; bulla with noticeable hyoidal groove, decidedly less than in examples of *O.* (*O.*) *alexi*; postglenoid process more massive than those of *O.* (*O.*) *bullatus*, less than those of *O.* (*O.*) *alexi*.

Mandible: Similar to examples of *O.* (*O.*) *bullatus*, ramus and ascending ramus with less depth than examples of *O.* (*O.*) *alexi*.

Dentition: Length of series intermediate in size between examples of *O.* (*O.*) *bullatus* and *O.* (*O.*) *alexi*; superior and inferior premolars average smaller than those of *O.* (*O.*) *alexi*; P^1–P^3 each with prominent anterior intermediate crest, more prominent than examples of *O.* (*O.*) *bullatus*, less robust than in *O.* (*O.*) *alexi*.

Limbs: Suggest approach in size to those of *O.* (*O.*) bullatus. (Known from fragmentary evidence.)

Measurements: Table 5 (p. 117).

Illustrations: Figures 11–13, 19–23.

Discussion

Leidy,[1] in the caption to plate 9, figure 4, of the original description of the new species *"Oreodon" hybridus*, identified the holotype as *"O. major."* The explanation for the same illustration on page 457 questioned it as a variety of *major* ("Variety of *O. major?*"), thus indicating the conclusion that it is close to that species. Leidy compared the species *hybridus* with *affinis* [=*Miniochoerus* (*Paraminiochoerus*) *affinis*[2]] and stated: "Figure 4, plate IX, represents a specimen nearly corresponding with the former one [*affinis*], but which in its proportions approaches *Oreodon major*[3] while the teeth are no longer than the usual in *Oreodon culbertsoni*."[4]

It is of interest that the holotypes of *M.* (*P.*) *affinis* and *Otionohyus* (*Otaraohyus*) *hybridus* are very similar in the skull portions preserved. The former, however, is considerably smaller. Examples of *O.* (*O.*) *hybridus* are smaller than those of *P.* (*B.*) *major*, and contain dentitions noticeably shorter and lighter, and approach those of *M. culbertsonii* as noted by Leidy.

Thorpe[5] stated, "The skull [of *O.* (*O.*) *hybridus*] is nearly as long as in *E. major* [=*Paramerycoidodon* (*Barbourochoerus*) *major*], but the zygomatic arches have a greater expansion." Later Thorpe[6] stated essentially the same. A size comparison of the larger, *P.* (*B.*) *major*, and the smaller, *O.* (*O.*) *hybridus*, is apparent in chart 2, present paper.

Thorpe also considered the skull Y.P.M.

[1] 1869.

[2] Schultz and Falkenbach, 1956, p. 405.

[3] This report, p. 92 = *Paramerycoidodon* (*Barbourochoerus*) *major*.

[4] This report, p. 38 = *Merycoidodon culbertsonii*.

[5] 1924b, p. 221.

[6] 1937, p. 77.

12609 as a plesiotype of *O.* (*O.*) *hybridus*. The longer dental series of this Colorado specimen seems closer to examples of *O.* (*O.*) *alexi* from "Zone D" of the Brule. The geologic occurrence of the holotype of *O.* (*O.*) *hybridus* is questionable (see following discussion), and the horizon of Thorpe's referred specimens are not known. The example F:A.M. 72009, as well as others from faunal "Zone C" of the Brule of South Dakota, readily compares with the holotype (also from South Dakota).

Leidy's[1] original description, based on Hayden's information, considered the three oreodont species *bullatus*, *hybridus*, and *affinis* as coming from "the lowest bed of the tertiary deposits of the Mauvaises Terres of the White River, or bed A of Hayden."

Sinclair[2] based some of his conclusions of oreodont occurrences on Leidy's and Hayden's individual reports. The present report contains a discussion on these facts under *Otionohyus* (*Otarohyus*) *bullatus* (p. 118).

The large oreodont collections now available do not contain examples from the Chadron that could possibly be referred to the three herein-mentioned species. Examples similar to the holotype of *O.* (*O.*) *hybridus* are found from the Brule faunal "Zone C," and it is here assumed that the holotype occurred in what is now considered "Zone C."

The present conclusion is that the species *O.* (*O.*) *hybridus* belongs to a separate phylum from that of *P.* (*B.*) *major* and is not a subspecies of the latter as suggested by Thorpe. *Otionohyus* (*O.*) *hybridus* appears to have been derived from *O.* (*O.*) *bullatus* which in turn gave rise to *O.* (*O.*) *alexi*.

The F:A.M. specimens were collected by Morris Skinner and party, 1938 and 1945.

Eleven specimens are here recorded:

HOLOTYPE

Anterior portion of skull with P^1–P^2 rt. and P^3(br.)–M^3 (P^4 only complete tooth). (w‡+)	A.N.S.P. 10860	From oreodont faunal "Zone C" of Brule Formation,[3] "Mauvaises Terres," South Dakota Figured by Leidy, 1869, pl. 9, fig. 14; Thorpe, 1937, fig. 38

REFERRED FROM (A) WASHABAUGH AND (B) JACKSON COUNTIES, SOUTH DAKOTA; AND (C) SHERIDAN COUNTY, NEBRASKA

A. FROM 18 MILES SOUTH OF KADOKA, WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

		F:A.M.
Skull with I^3–M^3 and mandible with I_2(rt.)–M_3. Figures 11–13	(w)	72009

B. FROM WHITE RIVER DRAINAGE, 1 TO 1½ MILES EAST OF NORBECK PASS,[4] JACKSON COUNTY, SOUTH DAKOTA

5 ASSOCIATED INDIVIDUALS

		F:A.M.
Partial left and right maxillae with P^3–M^3, partial mandible with I_1(rt.)–M_3 (I_2 br.), 2 partial humeri, partial radius, partial ulna, 2 femora (1 partial), and 2 tibiae (1 partial). Figures 19–22 (in part)	(w‡‡)	72011A
The above-listed limb elements are from a mature individual and presumably belong to F:A.M. 72011A which contains mature dentition.		
Skull with I^1–I^2 rt. and I^3–dP^2–M^3(erupt.) and mandible (attached) with I_3–dP_2–M_3 (germ)	(I)	72011B
Skull with I^1–dP^2–M^2 and mandible (attached) with I_1–I_3 br. and /C–dP_2–M_2	(I)	72011C
Partial skull with C/–dP^2–M^2 and partial mandible with /C(rt.)–dP_3–M_2(br.)	(I)	72011D
Partial left and right premaxillae and maxillae with I^2–I^3 alv., C/rt. and P^1–P^3 alv.		72011E

[1] 1869, p. 104.

[2] 1924, p. 102.

[3] The present writers assume that the holotype is from "Zone C" of the Brule Formation, since the referred material, which has associated geologic data, is from that faunal zone.

[4] Norbeck Pass is in the divide area between the White River and Bad River drainages.

3 partial scapulae, 2 partial humeri, 3 partial radii, 2 partial ulnae, partial tibia, 3 astragali, 4 calcanea (2 partial), partial pelvis, vertebrae, limb fragments, and manus and pes fragments. Figure 23 (in part)		F:A.M. 72011A–E

SKULL AND MANDIBLE

Partial skull with C/(br.)–M^3 and partial mandible (attached) with P_1(br.)–M_3 P_2 (alv.)	(M+)	72112

FROM 1½ MI. W. OF CEDAR PASS:

SKULL AND MANDIBLE

Partial skull with P^2(br.)–M^3 and partial mandible with P_2–M_3 (P_3 br.)	(w‡)	72010

C. TENTATIVELY REFERRED FROM WHITE RIVER DRAINAGE, 8 TO 10 MILES WEST OF WHITE CLAY, SHERIDAN COUNTY, NEBRASKA

SKULL AND MANDIBLE

Crushed partial skull with I^1–M^3 and partial mandible with /C(br.)–M_3	(w+)	F:A.M. 72012

The bullae of the above specimen are smaller than those of the holotype. The field records indicate that the specimen was derived from "an upper phase of *Leptauchenia* beds containing small nodules," so perhaps it came from a higher faunal zone.

3a. Otionohyus (Otarohyus) hybridus helenae (Douglass)

From deposits approximately equal in age to oreodont faunal "Zone C" of the Brule Formation, northeast of Toston, Broadwater County, Montana

Eucrotaphus helenae DOUGLASS, 1901b, p. 265.
Eporeodon helenae (Douglass): THORPE, 1937, p. 69, pl. 4, figs. 4–9.

CHARACTERS

SKULL: Approximate length of but wider than examples of *O.* (*O.*) *hybridus;* posterior border of nasals acute; lacrimal fossa smaller but deeper than in examples of *O.* (*O.*) *hybridus*; bulla approximately equal in size and prominence of hyoidal groove to those of *O.* (*O.*) *hybridus.* (Holotype is immature.)

MANDIBLE: Similar to examples of *O.* (*O.*) *hybridus* except for less width (lateral) of condyle.

DENTITION: Superior molars slightly wider (laterally) than examples of *O.* (*O.*) *hybridus*; inferior molars with prominent ridge on internal surface of anterior and posterior crescent. (Premolars known from deciduous dentitions only.)

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 117).

ILLUSTRATIONS: Figures 11–13.

DISCUSSION

Otionohyus (*Otarohyus*) *hybridus helenae* is known only from the immature type specimen. The exact geologic occurrence is not known, but the skull characters, including the size of the bulla and development of the hyoidal groove, compare with those of *O.* (*O.*) *hybridus* from "Zone C" of the Brule.

Douglass[1] considered the species *helenae* referable to the genus *Eucrotaphus,* and stated, "It was found northeast of Toston, in a bed of clay which contained nodular layers." He also described at the same time another species, "*Oreodon robustum*" [=*Merycoidodon macrorhinus* (Douglass)], from the same area but from a different geologic deposit, and reported that the holotype was "found in a bed of soft sandy clay, northeast of Toston." The holotype of this latter species, however, has a small (minute) bulla, similar to that in *M. culbertsonii,* but *O.* (*O.*) *h. helenae* has an inflated bulla.

This, at least, indicates that the two forms occurred in two separate stratigraphic units. The present writers believe that *M. macrorhinus* came from the lower unit (= "Zone A" of Brule) and *O.* (*O.*) *h. helenae* from the higher unit ("Zone C"). This conclusion is based on evidence concerning the development of the minute bullae (in all phyla of the Merycoidodontinae) of "Zone A" of the Brule into the inflated bullae found in the later faunal zones.

[1] 1901b, p. 243.

Thorpe[1] referred the species *helenae* to *Eporeodon* (see discussion of relationships of *Eporeodon*, p. 198; and *Eucrotaphus*, p. 165). He also considered the holotype skull equal in length to that of *Epigenetochoerus parvus* from the John Day. This is true, but a mature individual would be larger, and more like that of *O.* (*O.*) *hybridus*. Thorpe provisionally referred a skull, Y.P.M. 12447, from "South Dakota" (actually from Crow Butte near Crawford, Nebraska) to this species. He did note differences between the referred specimen and the holotype. The present writers, however, consider that this specimen should be referred to *Otionohyus* (*Otarohyus*) *bullatus*. (See p. 118.)

HOLOTYPE

Partial skull with dP^2–M^3 (erupt.) and partial mandible with P_1 (rt.)–P_2 (erupt.)–dP_3–M_3. (I)	C. M. 765	From oreodont faunal "Zone C"[2] of Brule Formation, NE. of Toston, Broadwater County, Montana; collected by Earl Douglass, 1898 Figured by Thorpe, 1937, pl. 4, figs. 4–8 This report, figures 11–13

4. **Otionohyus (Otarohyus) alexi,**[3] new species

From oreodont faunal "Zone D" of the Brule Formation, Washabaugh County, South Dakota; referred remains from Washabaugh, Jackson, Shannon, Pennington, and Harding counties, South Dakota; Sioux County, Nebraska; and tentatively referred from Jackson County, South Dakota; and Colorado

DESCRIPTION

SKULL: Largest of subgenus; lacrimal fossa deeper than examples of *O.* (*O.*) *hybridus* (from "Zone C" of Brule); bulla lacking prominent hyoidal groove; postglenoid process with tendency to be more massive than those of *O.* (*O.*) *hybridus*.

MANDIBLE: Ramus deep, deeper than examples of *O.* (*O.*) *hybridus*, with greatest increase below M_3.

DENTITION: Series heavier than in *O.* (*O.*) *hybridus;* P^1–P^3 each with strong and prominent anterior intermediate crest; P_3 with prominent posterior intermediate crest (well-preserved examples of P_1–P_2 not available).

LIMBS: (Unknown).

MEASUREMENTS: Table 5 (p. 117).

[1] 1937, p. 69.

[2] Faunal zone based on distribution of examples of this subgenus from other areas.

[3] Named in honor of Alex Kozikowski, a preparator of the Frick Laboratory.

ILLUSTRATIONS: Figures 11–13, 52.

DISCUSSION

Otionohyus (*Otarohyus*) *alexi* from "Zone D" of the Brule represents the end member of the subgeneric phylum. Actually the skulls of this species seem to have a tendency to be shallower (lower) than examples of *O.* (*O.*) *hybridus*, the ancestral species from "Zone C" of the Brule. The shallower skull and general appearance of examples of *O.* (*O.*) *alexi* are somewhat similar to examples of *Promesoreodon scanloni*,[4] also from "Zone D." The latter species has a wider skull, more inflated bulla, and larger teeth than does *O.* (*O.*) *alexi*, but could have been derived from the *O.* (*Otarohyus*) phylum, perhaps during the time of faunal "Zone C" of the Brule. This may be the link between the two subfamilies, the Promerycochoerinae (with examples from "Zone D" of the Brule through the Harrison formation) and the Merycoidodontinae (from "Zone B" of the Chadron through "Zone D" of the Brule).

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1938–1940, 1945; and the U.N.S.M. examples by C. Bertrand Schultz and associates.

Twenty-nine specimens are here recorded:

[4] Schultz and Falkenbach, 1949, p. 152, p. 21–25.

HOLOTYPE

Skull with C/(br.)–M^3. (M+) F:A.M. 72060 From oreodont faunal "Zone D" of Brule Formation, Craven Basin, 6–7 mi. N. of Wanblee, S. side of river, White River drainage, Washabaugh County, South Dakota; collected by Ralph Mefferd and Morris F. Skinner, 1940
Figures 12, 13, 52

REFERRED FROM (A) WASHABAUGH, (B) JACKSON, (C) SHANNON, (D) PENNINGTON, AND (E) HARDING COUNTIES, SOUTH DAKOTA; (F) SIOUX COUNTY, NEBRASKA; AND TENTATIVELY REFERRED FROM (G) JACKSON COUNTY, SOUTH DAKOTA; AND (H) COLORADO

A. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM HAY CREEK AREA:

2 SKULLS AND MANDIBLES

		F:A.M.
Partial skull with C/–P^1 rt. and P^2–M^3(br.) (P^4–M^1 br.) and partial mandible with P_2–M_3. Figure 11 (in part)	(W‡)	72065
Partial skull with P^2–M^1 br. and M^2–M^3 and mandible (attached) with P_1–P_4 rt. and M_1(br.)–M_3	(W+)	72317

FROM E. SIDE OF POTATO CREEK:

2 SKULLS AND MANDIBULAR RAMI

Skull with C/–M^3 and partial mandible (attached) with P_1(br.)–M_3	(W)	72113
Partial skull with dP^1–M^3(erupt.) (M^1 br. and M^2 alv.) and partial right ramus with M_2(br.)–M_3(erupt.)	(I)	72281

B. FROM WHITE RIVER DRAINAGE, JACKSON COUNTY, SOUTH DAKOTA

FROM E. SIDE OF CEDAR PASS:

SKULL AND MANDIBLE (ATTACHED)

		F:A.M.
Partial skull with C/(rt.)–M^3(br.) (P^1 and M^2 br.) and partial mandible (attached) with P_2 and M_1–M_3	(M+)	72062

FROM 1 MI. E. OF CEDAR PASS:

SKULL AND MANDIBULAR RAMI (ATTACHED)

Anterior portion of skull with I^1–M^3 and right ramus (attached) with /C–M_3	(W)	72063

FROM 1½ MI. NE. OF CEDAR PASS:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with P^1–M^3 and mandible (attached) with P_1(br.)–M_3	(W‡)	72095

FROM ¼ MI. W. OF CEDAR PASS:

SKULL AND MANDIBLE

Partial skull with P^2–M^3 and partial mandible with P_1–M_3(br.)	(W+)	72066

3 SKULLS

3 partial skulls with		
C/(rt.)–M^3 (P^2 rt.)	(M+)	72067
C/–M^3 (P^2 rt.)	(–M)	72068
I^1(alv.)–M^3 (I^2–P^1 br., P^3–P^4 erupt.)	(–M)	72069

FROM $2\frac{1}{2}$ MI. N. OF INTERIOR:

SKULL		F:A.M.
Partial skull with P^1–M^3 (P^2–P^4 erupt.)	(–M)	72072

C. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM S. SIDE OF SHEEP MT.:

SKULL, MANDIBLE, AND VERTEBRAE		F:A.M.
Crushed skull with P^1–M^3, mandible with P_1–M_3 (P_2 br.), and vertebrae	(w‡)	72061

SE. OF SHEEP MT., HEAD OF SPRING CREEK:

2 SKULLS AND MANDIBLES		
Partial skull with C/(rt.)–M^3 and partial mandible (attached) with P_1–M_3	(w)	72074
Partial skull with C/–M^3 (M^1–M^3 br.) and partial mandible with P_3(br.)–M_3(br.) (M_1–M_2 br.)	(w)	72316

C′. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM $1\frac{1}{4}$ MI. S. OF COTTONWOOD PASS,[1] BIG CORRAL DRAW AREA:

SKULL		F:A.M.
Skull with C/(rt.)–M^3	(w‡)	72071

FROM HEAD OF E. FORK OF BIG CORRAL DRAW:

2 SKULLS AND MANDIBLES		
Skull with C/–P^1 rt. and P^2(br.)–M^3 (P^3–M^1 br.) and mandible with I_1(br.)–M_3 (/C–P_1 br.)	(w+)	72070
Partial skull with I^2–M^3 and mandible (attached) with I_1–M_3	(w)	72089

FROM W. BIG CORRAL DRAW:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with C/(rt.)–M^3 (P^1 rt.) and partial mandible with P_1(alv.)–M_3 (P_2–P_3 br.)	(w)	72073

FROM NE. OF INDIAN STRONGHOLD:

SKULL AND MANDIBLE, IMMATURE		
Partial skull with C/(br.)–dP^2–M^2(br.) and partial mandible with /C(br.)–dP_2–M_2	(I)	72144

D. FROM WHITE RIVER DRAINAGE, NORTH SIDE OF PINNACLES,[2] PENNINGTON COUNTY, SOUTH DAKOTA

2 SKULLS		F:A.M.
Partial skull with M^2(br.)–M^3	(M)	72064
Partial skull with P^3(erupt.)–dP^4–M^3	(–M)	72146

E. FROM WHITE RIVER DRAINAGE, SLIM BUTTE AREA, HARDING COUNTY, SOUTH DAKOTA

SKULL		F:A.M.
Partial skull with I^1(alv.)–M^3	(w+)	72013

F. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–21:

SKULL		U.N.S.M.
Anterior right side of skull with C/–M^3	(w)	28171

[1] Cottonwood Pass is in the divide area between the Cheyenne River and White River drainages.
[2] In the divide area between the White River and Bad River drainages.

FROM U.N.S.M. COLL. LOC. SX-22: U.N.S.M.

SKULL

Partial skull with C/(br.)–M^3 (P^1 br.) . . . . (w+) 28202

G. TENTATIVELY REFERRED FROM WHITE RIVER DRAINAGE, 3½ TO 4 MILES NORTHWEST OF INTERIOR,[1] JACKSON COUNTY, SOUTH DAKOTA

MAXILLAE, MANDIBLE, AND ATLAS

Partial left and right maxillae with P^4–M^3 (M^1 br.), partial mandible with P_1–M_1(br.) and M_3, and atlas . . . . (w‡) F:A.M. 72237

The above specimen is not very complete, and exact identification is difficult. At the time it was collected, in 1938, the particular site was questioned as being "upper part of the Upper *Oreodon*" (="Zone C" of Brule) or "Lower *Leptauchenia* zone" (="Zone D" of Brule).

H. TENTATIVELY REFERRED FROM COLORADO (COLLECTED BY E. DEVENDORF AND COMPANY, 1873)

SKULL Y.P.M.

Partial skull with C/–P^2 br. and P^3–M^3 . . . . (w‡) 12609

The above skull was referred to *Eporeodon major hybridus* (Leidy) by Thorpe, 1937, p. 77; and Scott, 1940, p. 682.

The skull is far from complete, lacking the most important bulla.

IV. GENETOCHOERUS,[2] NEW GENUS

GENOTYPE: *Genetochoerus periculorum* (Cope).

DESCRIPTION

SKULL: Small in size, smallest skulls of subfamily; basal lengths ranging from 153 to 173 mm., widths from 84 to 112 mm.; dolichocephalic; medium high; supraoccipital wings small, not widely spread [more so than in examples of *G.* (*Osbornohyus*)], extended posteriorly for short distance posterior to condyles; sagittal crest light, moderately high [tendency to be lower than in skulls of *G.* (*Osbornohyus*)]; brain case long and narrow [more inflated in examples of *G.* (*Osbornohyus*)]; frontals moderately broad, similar to examples of *Merycoidodon*; nasals narrow [broader in those of *G.* (*Osbornohyus*)], posterior border almost acute; anterior nasal-maxilla above posterior border of C/; orbit roundish, medium size (smaller than orbits of *Merycoidodon*), directed outward, slightly forward and upward; malar shallow below orbit; zygomatic arch light; infraorbital foramen in area above P^3; lacrimal fossa large and moderately deep [deeper than in examples of *G.* (*Osbornohyus*)]; muzzle narrow; premaxillae touching but not joined; occipital condyles light [slightly heavier in examples of *G.* (*Osbornohyus*)]; paroccipital process long and light, anterior external surface excavated; bulla small (minute) [differing from the inflated bulla in examples of *G.* (*Osbornohyus*)], similar to all oreodonts from "Zone C" of Chadron and "Zone A" of Brule with exception of Leptaucheniinae, which possessed well-inflated bullae throughout the phylum; postglenoid process slightly robust [more so than in examples of *G.* (*Osbornohyus*)].

MANDIBLE: Moderately light; postsymphysis below P_3; ramus moderately shallow; ascending ramus moderately high; condyle small and light.

DENTITION: Light [lighter than examples of *G.* (*Osbornohyus*)]; approaching over-all length of some examples of Miniochoerinae (differing from that subfamily in possessing posteriorly produced paroccipital wings [not fan-shaped] and deep fossettes on molars); unworn C/ and P^1–P^3 each with prominent anterior intermediate crest; P^4 with suggested anterior intermediate crest; P_2–P_4 each with noticeable posterior intermediate crest.

LIMBS: Moderately short and light, shorter than examples of *Merycoidodon*, similar to those of *Otionohyus*, longer and more massive

[1] This locality is in the divide region between the White River and Bad River drainages.

[2] Ancestral hog.

than those of Miniochoerinae from "Zone A" of Brule; approaching length of but lighter than those of *Merychyus arenarum* from lower Marsland; example showing five digits on forefoot.

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

ILLUSTRATIONS: Figures 14–16, 52 (skulls, mandible, and dentitions), 19–23 (limbs).

DISCUSSION

The holotype of *Genetochoerus periculorum* (Cope), the genotypic species, was secured from Logan County, Colorado. There is a question as to the exact geological occurrence of the type specimen, but it compares well with material from Nebraska and Wyoming which was collected from sediments here considered as "Zone A" of the Brule.

Cope[1] and Gregory[2] considered the genoholotype of this new genus as referable to *"Oreodon."* Later, Thorpe[3] referred it to *Merycoidodon*. The smaller size of skull, the lighter teeth, and the smaller limb elements are diagnostically different from those of *Merycoidodon*. Examples of both *M. culbertsonii* and *G. periculorum* have small bullae and occur in "Zone A" of the Brule. The former species appears to have given rise to *M.* (*Anomerycoidodon*), whereas *G. periculorum* was ancestral to *G.* (*Osbornohyus*). Both subgenera have inflated bullae and have the same geologic distribution, i.e., from faunal zones "B" through "D" of the Brule. The relative size difference between examples of *M. culbertsonii* and those of *G. periculorum* is noted in the material from each faunal zone throughout the two phyla.

DISTRIBUTION

One species of *Genetochoerus* is known from Colorado, Nebraska, South Dakota, and Wyoming. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPE

One species of *Genetochoerus* from seven Brule (oreodont faunal "Zone A") localities are here recorded :

1. *Genetochoerus periculorum* (Cope), from Logan County, Colorado; referred remains from Niobrara and Converse counties, Wyoming; Scotts Bluff, Sioux, and Dawes counties, Nebraska; and Pennington and Shannon counties, South Dakota. ("Zone A" of Brule.)

HOLOTYPE: Skull and mandible, A.M. 6397. Figures 14–16, 52.

DETAILED LISTS OF TYPE, REFERRED SPECIMENS, AND SYNONYMY

GENETOCHOERUS

TOTAL AVAILABLE SPECIMENS: 43[4]

1. **Genetochoerus periculorum** (Cope)

From oreodont faunal "Zone A" of the Brule Formation, Logan County, Colorado; referred remains from Niobrara and Converse counties, Wyoming; Scotts Bluff, Sioux and Dawes counties, Nebraska; and Pennington and Shannon counties, South Dakota

Oreodon culbertsoni periculorum COPE, 1884a, p. 513. GREGORY, 1920, p. 188, fig. 156. WANLESS, 1923, p. 220, pl. 3, fig. 1.

Oreodon culbertsonii Leidy, in part: LEIDY, 1852a, pl. 10, figs. 5–6; 1854a, pl. 2, fig. 3, pl. 4, figs. 1–2.

Merycoidodon culbertsonii (Leidy), in part: HAY, 1902, p. 666.

Merycoidodon culbertsonii periculorum (Cope): THORPE, 1921f, p. 337; 1937, p. 55, pl. 3, figs. 1–2.

CHARACTERS

SKULL: Smaller than examples of *Merycoidodon culbertsonii*; larger than examples of any species of Miniochoerinae from "Zone A"; approaching length of some examples of *Otionohyus wardi*. (See generic description.)

MANDIBLE: Same size comparisons as with skull. (See generic description.)

DENTITION: Lightest dentition of the Merycoidodontinae from "Zone A" of the Brule. (See generic description.)

LIMBS: (See generic description.)

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

[1] 1884a, p. 511.
[2] 1920, p. 188.
[3] 1921f, p. 337.
[4] Includes 19 F:A.M. and 15 U.N.S.M. specimens.

ILLUSTRATIONS: Figures 14–16, 19–23, 52.

DESCRIPTION

Cope,[1] in the original description, and Gregory,[2] in a later reference to the species, considered this form a subspecies of *"Oreodon" culbertsonii.* Thorpe[3] agreed on the subspecies but changed the generic reference to *Merycoidodon.* The smaller skull, lighter teeth, and smaller limb elements of *G. periculorum* are distinct from those of *M. culbertsonii.* It is now apparent that examples of *G. periculorum,* with small bullae, from "Zone A" of the Brule gave rise to those of *G. (Osbornohyus) norbeckensis,* with an inflated bulla, from "Zone B." Also examples of *M. culbertsonii,* with small bullae, from "Zone A" of the Brule gave rise to those of *M. (Anomercoidodon) dani,* with inflated bullae, from "Zone B." This, of course, indicates that two forms represent two separate phylogenetic lines ranging from zones "A" through "D" of the Brule.

Thorpe's conclusions were: "This subspecies [*M. culbertsonii periculorum*] probably should be considered as a geographic variant or mutant confined mainly to Colorado, although a few specimens have been collected in Wyoming and Nebraska. Except for its smaller size, it differs so little from *M. culbertsonii* that it might well be considered as the female form of that species, but geographic distribution seems opposed to this conclusion." Actually, at the present time, the species is better known from Wyoming, Nebraska, and South Dakota than from Colorado.

The genus *Merycoidodon* has long been used as a "catch-all" for the Brule oreodonts. The species *Genetochoerus periculorum, Miniochoerus (Paraminiochoerus) affinis, M. (P.) gracilis,* and *Platyochoerus platycephalus* were all referred to *Merycoidodon* before the present writers reported on the Miniochoerinae.[4] Not only were these forms generically distinct from *Merycoidodon,* but they actually belong to two different subfamilies. Evidently the stratigraphy was not considered or not known by most of the workers, or perhaps adequate geologic data concerning the specimens were not available. As a result, a horizontal classification was used, since these forms have superficial characters in common. The oreodonts from the middle Oligocene deposits are close to the point of divergence. Thus classification is difficult, and in many instances it is almost impossible to separate the forms into their respective phyla without a consideration of material from the various faunal zones of the Brule. (See comparisons of Merycoidodontinae and Miniochoerinae, p. 28.)

Leidy[5] referred an example (U.S.N.M. 137) to *Merycoidodon culbertsonii,* but this particular specimen is here referred to *Genetochoerus periculorum.*

Boardman Bump and F. B. Loomis[6] reported on variation in the following four species of oreodonts and referred these all to *Merycoidodon: affinis* and *gracilis* [*Miniochoerus (Paraminiochoerus)*], *periculorum* (=*Genetochoerus*), and *culbertsonii* (=*Merycoidodon*). In 1956 (p. 388) Schultz and Falkenbach discussed the first two species, and they consider the latter two in the present report (p. 29).

Examples of *Genetochoerus periculorum* and *Merycoidodon culbertsonii* possess posteriorly projecting supraoccipital wings and deep molar fossettes and are considered to be of the same subfamily (Merycoidodontinae). Therefore, it is understandable why Bump and Loomis included these two species under the same genus. *Miniochoerus (Paraminiochoerus) gracilis* and *M. (P.) affinis,* however, have fan-shaped occipital regions and shallow molar fossettes and are considered by the present writers to belong in the subfamily Miniochoerinae.

In remains of the Miniochoerinae, regardless of the faunal-zone occurrence, the bullae remain small (minute) so that like forms from above "Zone A" of the Brule might well have been included in the Bump and Loomis study. This inclusion of examples from more than one faunal zone could not readily be detected unless the geologic occurrence of each form was known. In both the *Merycoidodon* and *Genetochoerus* phyla, however, the bullae are small in "Zone A" of the Brule and inflated above that zone. Thus in the last two phyla, it is assumed that Bump and Loomis did not in-

[1] 1884a, p. 511.
[2] 1920, p. 180, fig. 156.
[3] 1937, pp. 55-56.
[4] Schultz and Falkenbach, 1956, p. 388.
[5] 1852a and 1854a.
[6] 1930, p. 17; see also Schultz and Falkenbach, 1956, p. 388.

clude specimens from above faunal "Zone A" of the Brule.

Bump and Loomis further postulated that remains of *G. periculorum* "might be the female of *M. culbertsonii.*" However, they concluded, "The only objection is in that, numerically, they should be more nearly equal." The present writers differ considerably from Bump and Loomis concerning possible sex variation for the following reasons: (1) the two species include sufficient ranges of individual variation which do not overlap; (2) the skull and skeletal elements of *G. periculorum* are decidedly smaller and lighter than those of *M. culbertsonii,* too much so to be considered as representing sex variation (i.e., in a subfamily where sex variation is slight, if at all apparent); (3) examples of *G. periculorum* have comparatively light dentitions in contrast to those of *M. culbertsonii.*

Sinclair[1] considered *G. periculorum* a subspecies of *M. culbertsonii* and reported that three examples had been secured from the "Lower Nodular Zone" and one from the "Upper Nodular Zone." The difficulty here is that the specimens were not cited by catalogue numbers; therefore it is difficult to confirm Sinclair's identifications. The type of bullae would determine the identifications.

A referred specimen, F:A.M. 49730, is virtually a complete skeleton and remarkably well preserved. The preparation of this skeleton by Mr. Frank Miller (deceased) of the Frick Laboratory is outstanding; Miller's careful work yielded the small metacarpal I.

The F:A.M. specimens from Wyoming were collected by Charles H. Falkenbach and associates, 1938–1944; from South Dakota, by Morris F. Skinner and associates, 1938, 1939, 1951; from Nebraska, by Morris F. Skinner, Charles H. Falkenbach, and associates, 1944; and the U.N.S.M. material was collected by C. Bertrand Schultz and associates, 1933–1941, 1945–1952.

Forty-four specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3 and mandible with I_1–M_3. (M+)	A.M. 6397	From oreodont faunal "Zone A" of Brule Formation,[2] Horsetail Creek, Logan County, Colorado Figured by Gregory, 1920, fig. 156; Thorpe, 1937, pl. 3, figs. 1–2 This report, figures 14–16, 52

REFERRED FROM (A) LOGAN COUNTY, COLORADO; (B) NIOBRARA AND (C) CONVERSE COUNTIES, WYOMING; (D) SCOTTS BLUFF, (E) SIOUX, AND (F) DAWES COUNTIES, NEBRASKA; (G) PENNINGTON AND (H) SHANNON COUNTIES, SOUTH DAKOTA

A. FROM HORSETAIL CREEK, LOGAN COUNTY, COLORADO

SKULL AND MANDIBLE		A.M.
Skull with I^1–M^3 and mandible with I_1–M_3	(w)	6399

B. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, NIOBRARA COUNTY, WYOMING

FROM SPRING DRAW:

SKULL AND MANDIBLE		F:A.M.
Partial skull with P^2–M^3 and partial mandible with P_2–M_3	(w‡)	45082

FROM SHACK DRAW:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with I^1–M^3, mandible with I_1–M_3, partial scapula, humerus, radius, ulna, partial femur, pelvis, vertebrae, and ribs	(w)	49741

[1] 1924, p. 102.

[2] The present writers assume that the holotype is from oreodont faunal "Zone A" of the Brule Formation, since the referred material, which has associated geologic data, is from the faunal zone.

SKULL AND MANDIBULAR RAMUS — F:A.M.

Skull with I^1(rt.)–M^3 and partial left ramus with M_1–M_3 . . . . (W) 49724

4 SKULLS

Four skulls with
I^3(br.)–dP^3–M^3 (P^2–P^3 erupt.) and atlas . . . . (–M) 49725
C/(br.)–M^3. . . . . (M+) 49726
I^1–I^3 rt. and C/–M^3 . . . . (W) 49727
I^1–I^3 alv. and C/–M^3 . . . . (W) 49728

C. FROM NORTH PLATTE RIVER DRAINAGE, 8 MILES SOUTHEAST OF DOUGLAS, CONVERSE COUNTY, WYOMING

SKULL — U.N.S.M.

Partial skull with C/–P^2 rt. and P^3–M^3. (W‡) 28147

D. FROM NORTH PLATTE RIVER DRAINAGE, U.N.S.M. COLL. LOC. SF–101, SCOTTS BLUFF COUNTY, NEBRASKA

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS — U.N.S.M.

Partial skull with I^2–C/ rt. and P^1(br.)–M^3 (P^3 and M^1–M^2 br.), mandible with I_1–/C rt. and P_1–M_3 . . . . (W‡) 28337
2 partial scapulae, 2 partial humeri, partial radius, partial ulna, femur, 3 partial tibiae, partial pes, vertebrae, and ribs 28337A
Partial skull with I^1–M^3 (C/ br.), mandible with I_1–M_3 . . . . (M+) 28338
Partial scapula, 2 humeri (1 partial), 2 radii (1 partial), 2 ulnae (1 partial), tibia, 2 astragali, 2 calcanea, 2 partial pedes, vertebrae, and ribs 28338B

SKULL

Partial skull with I^1(alv.)–M^3 . . . . (W+) 28475

E. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–4:

SKULL AND MANDIBLE (ATTACHED) — U.N.S.M.

Partial skull with P^2–M^3 and mandible with I_1–/C rt. and P_1–M_3 . . . . (M) 28085

FROM U.N.S.M. COLL. LOC. SX–5 (=F:A.M. COLL. LOC. "10 MI. N. OF HARRISON, 2½ MI. E. OF WARBONNET CREEK, W. END"):

SKULL

Partial skull with C/(rt.)–M^3 . . . . (M+) 28168

SKULL AND MANDIBLE (ATTACHED) — F:A.M.

Partial skull with P^1–M^3 and mandible with P_1(br.)–M_3 . . . . (–M) 49731

FROM U.N.S.M. COLL. LOC. SX–6:

Partial skull with P^1–dP^3–M^3(germ) and mandible (left ramus attached) with dP_3–M_3 (germ) . . . . (I) U.N.S.M. 28474

FROM 10 MI. N. OF HARRISON (=U.N.S.M. COLL. LOC. SX–6 AND 7):

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS — F:A.M.

Skull with I^1–M^3, mandible with I_1(rt.)–M_3, 2 scapulae, 2 humeri, 2 radii, 2 ulnae, 2 manus (5-toed), 2 femora, 2 tibiae, 2 astragali, 2 calcanea, 2 pedes (4-toed), pelvis, vertebrae, and ribs. Figures 14–16, 19–23, 52 . . . . (W‡) 49730
Skull with I^1–dP^3–M^3(germ), mandible with I_1–dP_4–M_3(germ), 2 partial femora, 2 tibiae (1 partial), 2 astragali, calcaneum, and vertebrae . . . . (I) 49732

FROM U.N.S.M. COLL. LOC. SX–12:

		U.N.S.M.
Partial skull with C/(rt.)–P^1–M^3 and mandible (attached) with P_1(rt.)–M_3	(w‡+)	28032

FROM U.N.S.M. COLL. LOC. SX–37:

SKULL AND MANDIBLE (IMMATURE)

Partial skull with I^1–dP^2–M^2 and mandible with I_1–dP_2–M_2	(I)	28070

FROM "HAT CREEK, NEBRASKA,"[1] 1894:

SKULL

		A.M.
Skull with I^1–M^3 (I^2 rt.)	(w‡)	1291

Osborn's reference to this catalogue number was a typographical error.[2]

E′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–17:

SKULL AND MANDIBLE (ATTACHED)

		U.N.S.M.
Partial skull with I^1–I^3 alv. and C/(rt.)–M^3 and mandible with I_1–M_3 (/C rt.) . .	(w)	28133

FROM U.N.S.M. COLL. LOC. SX–24:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with C/(rt.)–M^3 (P^1–P^2 br.) and mandible with I_1–/C rt. and P_1(br.)–M_3	(w)	28079

The inferior border of the malar of the above specimen has an unusually abrupt and deep downward curve.

FROM U.N.S.M. COLL. LOC. SX–25:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with I^1–I^3 br. and C/–M^3 and mandible with I_1(alv.)–M_3 (I_2 br.) . .	(M)	28073

FROM U.N.S.M. COLL. LOC. SX–29:

SKULL AND MANDIBULAR RAMUS (IMMATURE)

Skull with I^1–dP^2–M^3(germ) and left ramus with I_1–I_3 br. and /C–dP_2–M_3(germ) .	(I)	28148

F. FROM WHITE RIVER DRAINAGE, 2 MILES NORTH OF CHADRON,[3] DAWES COUNTY, NEBRASKA

SKULL AND MANDIBLE

Anterior portion of skull with I^1–M^3 and fragmentary mandible with I_1–I_3 br. and /C(br.)–M_3 (P_3 br. and P_4 alv.)	(w)	F:A.M. 72285

Field records indicate that this specimen was found "110′ above Blue Ash," so it may be from a higher oreodont faunal zone.

G. FROM CHEYENNE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM 1 MI. N. OF SHEEP MOUNTAIN:

SKULL AND MANDIBLE (ATTACHED)

		F:A.M.
Partial skull with I^1–I^2 rt. and I^3–M^3 and mandible with I_1–M_3	(w)	49743

FROM "ENTELODONT PEAK," BASIN OF INDIAN CREEK (COLLECTED BY W. S. SINCLAIR, 1920):

SKULL AND MANDIBLE (ATTACHED)

		P.U.
Skull with I^2–dP^2–M^2 and mandible with I_1(br.)–dP_3–M_2	(I)	12525

[1] Exact locality unknown to present writers.
[2] 1918, p. 112.
[3] = U.N.S.M. Coll. Loc. DW–105.

FROM BEAR CREEK BASIN (COLLECTED BY H. R. WANLESS, 1920):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		P.U.
Skull with I^3–M^3 (C/ br.), mandible with I_2–M_3, and most of skeleton	(W+)	12565

The above specimen has five digits on the manus.

G′. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM IMLAY AREA:

2 SKULLS		F:A.M.
Partial skull with C/–P^1 rt. and P^2–M^3	(W)	45101
Partial skull with P^2–M^3	(W+)	45218

FROM EAST SIDE OF SADDLE HORSE PASS:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with P^3–M^3 and partial mandible with M_2–M_3.	(W)	45022

FROM 2 MI. W. OF CONATA:

SKULL		
Partial skull with P^1–dP^2(br.)–M^3(erupt.)	(I)	72230

FROM SCENIC AREA[1]:

SKULL AND MANDIBLE		A.M.
Partial skull with I^3–M^3 and mandible with /C–M_3	(M‡)	39462
SKULL		
Partial skull with C/(br.)–M^3.	(W+)	48820

H. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1 MI. N. OF COTTONWOOD PASS (BIG CORRAL DRAW AREA):

SKULL AND MANDIBLE (ATTACHED), IMMATURE		F:A.M.
Anterior portion of skull with I^1(rt.)–dP^2–M^2 (I^3 br.) and partial mandible with I_1–/C br. and dP_2–M_2	(I)	72229

FROM 1½ MI. S. OF COTTONWOOD PASS (BIG CORRAL DRAW AREA):

SKULL		
Partial skull with I^1–C/ rt. and P^1–M^3	(W+)	45021

FROM BETWEEN BIG AND LITTLE CORRAL DRAWS:

SKULL AND MANDIBLE (ATTACHED)		
Skull with I^1–I^2 br. and I^3–M^3 and mandible with I_1–P_2 rt. and P_3–M_3	(W)	45019

FROM HEAD OF QUINN DRAW:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with I^2(rt.)–M^3 and partial mandible with P_3–M_3	(W+)	49742

H′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM COTTONWOOD CREEK (COLLECTED BY H. R. WANLESS, 1922):

SKULL AND MANDIBLE (ATTACHED)		P.U.
Partial skull with I^1(rt.)–M^3 (C/ br.) and mandible with I_1(rt.)–M_3 (I_2–/C br.) . .	(W+)	12759

[1] Actual drainage is questionable.

H″. FROM "SOUTH DAKOTA"[1] (COLLECTED BY JOHN EVANS)

SKULL AND MANDIBLE (ATTACHED)	U.S.N.M.
Partial skull with P^1–M^3 and mandible with /C–P_1 br. and P_2–M_3. . . . . (w+)	137

Figured by Leidy, 1852a, pl. 10, figs. 5–6; 1854a, pl. 2, fig. 3; pl. 4, figs. 1–2.
Leidy referred this specimen to *Merycoidodon culbertsonii.*

IVA. GENETOCHOERUS (OSBORNOHYUS), NEW SUBGENUS

SUBGENOTYPE: *Genetochoerus* (*Osbornohyus*) *geygani,* new species.

DESCRIPTION

SKULL: Small in size; dolichocephalic; basal length ranging from 163 to 180 mm., width from 98 to 118 mm.; similar to characters of *Genetochoerus* except for following: larger size, sagittal crest not so prominent, supraoccipital wings more widely spread, nasals broader, lacrimal fossa smaller and of less depth (change is progressively shallower in later geologic sequence), occipital condyles slightly heavier, postglenoid process more robust, and bulla more inflated.

MANDIBLE: Same characters as *Genetochoerus* except for larger size and being more robust.

DENTITION: Same characters as *Genetochoerus* except more robust.

LIMBS: Same characters as *Genetochoerus* except for being slightly longer and more robust.

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

ILLUSTRATIONS: Figures 14–16, 52 (skulls, mandibles, and dentitions), 19–23 (limbs).

DISCUSSION

Genetochoerus (*Osbornohyus*) represents a continuation of the *Genetochoerus* phylogenetic line. The well-inflated bullae of the subgenus differ greatly from the small (minute) examples of the genus. There is a gradual increase in the size of the skulls and in the robustness of the dentitions of *G.* (*Osbornohyus*) from each successive stratigraphic layer in the geologic sequence (from faunal zones "B" through "D" of the Brule). The phylum of *Genetochoerus-G.* (*Osbornohyus*) actually seems to represent a more conservative group within the Merycoidodontinae.

It is of interest that two John Day genera, *Pseudogenetochoerus* and *Epigenetochoerus,* seem to be closer to *G.* (*Osbornohyus*) than to any of the other oreodonts. The *Genetochoerus* (*Osbornohyus*) line became extinct in the Great Plains at the end of the Oligocene. At least, no remains representing this subgenus are found in deposits later in age than faunal "Zone D" of the Brule. *Pseudogenetochoerus* and *Epigenetochoerus* are both known only from the John Day deposits of Oregon, and the examples of these two genera are here considered to be the same geologic age as the Harrison of the Great Plains. The skulls of *Pseudogenetochoerus* are slightly larger than those of the largest examples of *G.* (*Osbornohyus*). The size difference, however, is not what might be expected between two related forms from faunal "Zone D" of the Brule and from the John Day horizon, which appears to be equivalent in age to the Harrison.

Examples of *Epigenetochoerus parvus* from the John Day are the same size as those of *Genetochoerus periculorum.* The two forms also have many characters in common. This John Day species may represent a dwarf of the subfamily. Of course, there is even a possibility that *Epigenetochoerus* is more closely related to the Desmatochoerinae.

The possible relationship of the John Day oreodonts with those of the Great Plains is discussed on pages 199 and 402. It is difficult to realize that mammals of the size of the John Day oreodonts were isolated for a considerable period of time, but evidence at hand indicates that at least certain phylogenetic lines (representing small to medium-sized forms) developed independently in the Oregon region, and perhaps even evolved at a slower rate than did parallel or closely related lines in the Great Plains.

The proposed sequence of the species of *Genetochoerus* (*Osbornohyus*) is as follows: *G.* (*O.*) *norbeckensis* from "Zone B," *G.* (*O.*) *geygani* from "Zone C," and *G.* (*O.*) *chamberlaini* from "Zone D," all of the Brule. *Geneto-*

[1] Exact locality unkown to writers.

choerus (*O.*) *dickinsonensis* is also from "Zone D" of the Brule, perhaps a side line.

DISTRIBUTION

Four species of *Genetochoerus* (*Osbornohyus*) are known from Nebraska, North Dakota and South Dakota. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

Four species of *Genetochoerus* (*Osbornohyus*) from three Oligocene localities are here recorded:

1. *Genetochoerus* (*Osbornohyus*) *norbeckensis,* new species, from Jackson County, South Dakota; referred remains from Pennington and Shannon counties, South Dakota; and Sioux county, Nebraska; and tentatively referred from Stark County, North Dakota. (Oreodont faunal "Zone B" of Brule.)

HOLOTYPE: Skull, ramus, and skeletal elements, F:A.M. 49733. Figures 14–16, 21, 22, 52.

2. *G.* (*Osbornohyus*) *geygani,* new species, from Shannon County, South Dakota; referred remains from Shannon, Jackson, and Washabaugh counties, South Dakota; and tentatively referred from Shannon County, South Dakota; and Stark County, North Dakota. ("Zone C" of Brule.)

HOLOTYPE: Skull, mandible, and skeletal elements, F:A.M. 49734. Figures 14–16, 20, 22, 23.

3. *G.* (*Osbornohyus*) *chamberlaini,* new species, from Sioux County, Nebraska; referred remains from Sioux County, Nebraska; and Shannon and Jackson counties, South Dakota; and tentatively referred from Shannon County, South Dakota. ("Zone D" of Brule.)

HOLOTYPE: Skull and mandible, U.N.S.M. 28340. Figures 14–16.

4. *G.* (*Osbornohyus*) *dickinsonensis* (Douglass), from Stark County, North Dakota. ("Zone D" of Brule.)

HOLOTYPE: Skull, mandible, and skeletal elements, C.M. 1584. Figures 14–16, 19, 20, 22, 52.

DETAILED LISTS OF TYPES AND REFERRED SPECIMENS AND SYNONYMY

GENETOCHOERUS (OSBORNOHYUS)

TOTAL AVAILABLE SPECIMENS: 52[1]

1. Genetochoerus (Osbornohyus) norbeckensis,[2] new species

From oreodont faunal "Zone B" of the Brule Formation, Jackson County, South Dakota; referred remains from Pennington and Shannon counties, South Dakota; and Sioux County, Nebraska; and tentatively referred from Stark County, North Dakota

DESCRIPTION

SKULL: Slightly larger than examples of *G. periculorum*; smallest basal length in subgenus; posterior border of nasals acute; infraorbital foramen in area above mid to posterior portion of P^3; lacrimal fossa small but deep; malar below orbit with less depth than average examples of subgenus; bulla well inflated, with deep and prominent hyoidal groove (more prominent than in other examples of subgenus).

MANDIBLE: Same size range as skull; similar to examples of *G. periculorum*; lighter than in other examples of subgenus; postsymphysis below mid portion of P_3.

DENTITION: Lightest and smallest of subgenus, approximately equal to that of genus; P^1–P^3 each with moderately strong anterior intermediate crest.

LIMBS: Similar to and within size range of examples of *G. periculorum,* lighter than examples of *G.* (*O.*) *geygani.*

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

ILLUSTRATIONS: Figures 14–16, 21–23, 52.

DISCUSSION

Remains of *Genetochoerus* (*Osbornohyus*) *norbeckensis* are not so well represented in the collections as are those of *Genetochoerus periculorum.* The skulls of the former are slightly larger than and possess other characters in common with those of *G. periculorum,* except for the well-inflated bullae which differ considerably from the minute bullae of *G. periculorum.* The dentition is within the size range of examples of *G. periculorum* from

[1] Includes 48 F:A.M. and 2 U.N.S.M. specimens.

[2] Named after Norbeck Pass, Jackson County, South Dakota.

TABLE 6

Genetochoerus (*Osbornohyus*), NEW SUBGENUS, *Pseudogenetochoerus*, NEW GENUS, AND *Epigenetochoerus*, NEW GENUS. COMPARATIVE MEASUREMENTS[a] OF SKULLS AND MANDIBULAR RAMI

SKULL	*G. (O.) norbeckensis*, new species	*G. (O.) geygani*, new species	*G. (O.) chamberlaini*, new species	*G. (O.) dickinsonensis* (Douglass)	*P. condoni* (Thorpe)	*P. covensis*, new species	*E. parvus* (Thorpe)
	Holotype F:A.M. 49733	Holotype F:A.M. 49734	Holotype U.N.S.M. 28340	Holotype C.M. 1584	Holotype Y.P.M. 11016	Holotype A.M. 7509	Holotype Y.P.M. 12425
Stage of wear of teeth	(W+)	(W+)	(W‡)	(M+)	(W)	(W‡)	(W‡⁺)
Length (incl. supraoccipital crest and incisors)	((194))	202	((204))	((195))	((218))	225	((183))
Basal length (from anterior notch of foramen magnum to posterior base of I^1	((165))	169	((178))	175	185	195.5	—
Width (max.)	((98))	118	—	(110)	(122)	120	—
Width of brain case (max.)	53	54.5	55.5	59	64	62	49
Width, interorbital (min.)	(52)	(56)	47	(56)	51.5	53.5	—
Distance from anterior rim of orbit to anterior base of C/	69	75	71	74	80.5	76.5	75
Distance from anterior rim of orbit to supraoccipital crest	(117)	125	126.5	—	135.5	144	(105)
Length of nasals	—	73.5	—	—	—	80.5	—
Width of muzzle at infraorbital foramina	45.5	46	42	47	55	54	—
Width across canines	32	41	((38))	—	43	46.5	—
Length, C/–M^3 incl.	91	96	97	92	93.5	95	80.5
Length, P^1–M^3 incl.	78	81	81	79.5	80	82.5	70
Length, P^1–P^4 incl.	40	39.5	39	39	40.5	40.5	35
Length, M^1–M^3 incl.	40.5	43.5	(44)	41.5	41.5	43	37
Width of M^3 (max.)	17.5	18.5	18	15.5	18	17	—
Depth of malar below orbit	14.5	16.5	18	13.5	16	17.5	17.5

TABLE 6—(*Continued*)

MANDIBULAR RAMUS	*G.* (*O.*) *norbeckensis*, new species	*G.* (*O.*) *geygani*, new species	*G.* (*O.*) *chamberlaini*, new species	*G.* (*O.*) *dickinsonensis* (Douglass)	*P. condoni* (Thorpe)	*P. covensis*, new species	*E. parvus* (Thorpe)
	Holotype F:A.M. 49733	Holotype F:A.M. 49734	Holotype U.N.S.M. 28340	Holotype C.M. 1584	Referred U.C. 1910	Holotype A.M. 7509	Holotype Y.P.M. 12425
Stage of wear of teeth					(w‡)		
Length (max., incl. incisors)	—	143	—	158	179.5	170	—
Length, /C-condyle incl.	—	131	—	148	—	156.5	—
Depth of jaw under coronoid	—	62.5	—	—	—	80	—
Depth of jaw below anterior edge of M_3	(32)	34.5	39	31	37.5	32.5	33
Length, /C–M_3 incl.	87.5	94	—	95.5	100	100.5	85
Length, P_1–M_3 incl.	82.5	88.5	—	86.5	91.5	90.5	79.5
Length, P_1–P_4 incl.	37	40.5	—	40	42.5	43	34
Length, M_1–M_3 incl.	45.5	49	50	46.5	49	49.5	46.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

TABLE 7

Merycoidodon LEIDY, *Merycoidodon* (*Anomerycoidodon*), NEW SUBGENUS, *Merycoidodon* (*Blickohyus*), NEW SUBGENUS, *Paramerycoidodon*, NEW GENUS, *Paramerycoidodon* (*Gregoryochoerus*), NEW SUBGENUS, *Paramerycoidodon* (*Barbourochoerus*), NEW SUBGENUS, *Otionohyus*, NEW GENUS, *Otionohyus* (*Otarohyus*), NEW SUBGENUS, *Genetochoerus*, NEW GENUS, *Genetochoerus* (*Osbornohyus*), NEW SUBGENUS, AND *Epigenetochoerus*, NEW GENUS. COMPARATIVE MEASUREMENTS[a] OF SKELETAL ELEMENTS

	Length of Humerus (Articular)	Length of Radius (Articular)	Length of Ulna (Maximum)	Length of Metacarpal III (Maximum)	Length of Femur (Articular)	Length of Tibia (Articular)	Length of Metatarsal III (Maximum)	Length of Calcaneum (Maximum)
M. forsythae, new species, referred, F:A.M. 72325	—	99.5	129	50	(143)	126	63.5	46
M. culbertsonii (Leidy), referred	154[b]	128.5[b]	176.5[b]	57[c]	168[d]	143[d]	69[d]	57[d]
M. c. browni, new subspecies, holotype, F:A.M. 72286	141	122.5	162	62.5	166	145.5	71	58.5
M. c. osborni, new subspecies, holotype, F:A.M. 49668	142.5	116	159	61	168	147	71	61
M. (*A.*) *dani*, new species, referred, F:A.M. 72138	—	110	—	—	—	—	—	54
M. (*A.*) *lambi*, new species, holotype, F:A.M. 72139	—	123.5	(173)	63.5	174	144	—	59
M. (*B.*) *lynchi*, new species, holotype, F:A.M. 72114	(144)	—	—	—	162	140.5	(74)	57.5
P. georgei, new species, referred, F:A.M. 72209	—	131	175	—	—	—	—	—
P. (*B.*) *major* (Leidy), referred, F:A.M. 45298	152.5	126	174	59.5	182	151	—	58.5
P. (*G.*) *meagherensis* (Koerner), holotype, Y.P.M. 13948	—	—	—	—	—	—	67	—
O. wardi, new species, holotype, F:A.M. 49662	125	101.5	137.5	56[e]	142.5[f]	(120)	62	48.5[g]

TABLE 7—(*Continued*)

	Length of Humerus (Articular)	Length of Radius (Articular)	Length of Ulna (Maximum)	Length of Metacarpal III (Maximum)	Length of Femur (Articular)	Length of Tibia (Articular)	Length of Metatarsal III (Maximum)	Length of Calcaneum (Maximum)
O. w. degrooti, new subspecies, holotype, F:A.M. 49760	(122)	103.5	140	52	148	131	?	59
?*O. vanderpooli*, new species, holotype, F:A.M. 49766	123	—	—	—	—	(126)	—	—
O. (*O.*) *bullatus* (Leidy), referred	139[h]	116.5[i]	—	59[j]	159.5[h]	135.5[h]	71.5[i]	56[i]
O. (*O.*) *cedrensis* (Matthew), holotype, A.M. 8949[k]	128	98	142	(49)	—	—	—	—
G. periculorum (Cope), referred, F:A.M. 49730	123.5	106.5	142.5	51	148.5	128.5	62	49
G. (*O.*) *norbeckensis*, new species, holotype, F:A.M. 49733	—	—	—	—	143.5	128.5	—	—
G. (*O.*) *geygani*, new species, referred, F:A.M. 49789	131	—	—	—	—	—	—	—
G. parvus (Thorpe), referred, A.M. 7588	128	107.5	140.5	—	147	135	49	65

[a] ( ), Approximate All measurements in millimeters.
[b] F:A.M. 72186A.
[c] U.N.S.M. 28467.
[d] F:A.M. 45159.
[e] F:A.M. 72040.
[f] F:A.M. 45044.
[g] F:A.M. 45468A.
[h] F:A.M. 45267.
[i] F:A.M. 45268.
[j] F:A.M. 45176A-B.
[k] Immature individual.

"Zone A" of the Brule but is smaller than that of *G.* (*O.*) *geygani* from "Zone C," the latter also having more robust series.

The holotype of *G.* (*O.*) *norbeckensis*, F:A.M. 49733, includes a femur, slightly shorter, and a tibia, considerably shorter, than examples of *G. periculorum*. These are the only comparable limb elements of the species. In comparison with the fragmentary limb elements of *G.* (*O.*) *geygani*, those of *G. periculorum* and *G.* (*O.*) *norbeckensis* are lighter.

The F:A.M. specimens from South Dakota were collected by Morris F. Skinner and associates, 1938, 1939, 1945; from North Dakota, by Morris F. Skinner and associates, 1944; and the U.N.S.M. specimen was collected by C. Bertrand Schultz and associates, 1936.

Eleven specimens are here recorded:

HOLOTYPE

Partial skull with C/–M^3, partial left ramus with I_1–/C rt. and P_1–M_3, femur, and tibia. (W+)	F:A.M. 49733	From oreodont faunal "Zone B" of Brule Formation, "Top of Middle *Oreodon*," Norbeck Pass,[1] Jackson County, South Dakota; collected by Ove Kaisen, Leonard Nelson, Morris F. Skinner, Morris F. Skinner, Jr., 1945 Figures 14–16, 21, 22, 52

REFERRED FROM (A) PENNINGTON AND (B) SHANNON COUNTIES, SOUTH DAKOTA; (C) "CHEYENNE RIVER," SOUTH DAKOTA; (D) SIOUX COUNTY, NEBRASKA; AND (E) STARK COUNTY, NORTH DAKOTA

A. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM W. SIDE OF NORBECK PASS:

SKULL, MANDIBLE, AND ASTRAGALUS, IMMATURE

Partial skull with P^2–dP^3–M^3, mandible with P_2–dP_3–M_3(br.), and astragalus. Figure 23 (in part) . . . . (I) F:A.M. 49759

FROM 4 MI. SE. OF SCENIC:

SKULL AND MANDIBLE

Partial skull with C/(rt.)–M^3 and mandible with I_1(rt.)–M_3 (I_2 br.) . . . . (M+) 45278
Posterior border of nasal is acute.

B. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM E. SIDE OF HARNEY SPRINGS:

MANDIBLE F:A.M.

Partial mandible with P_1–P_2 rt. and P_3–M_3 . . . . (W) 45359

FROM ¾ MI. E. OF CEDAR BLUFFS:

SKULL

Partial skull with I^1–I^3 rt. and C/(br.)–M^3 . . . . (W) 45353

MANDIBULAR RAMUS

Partial left ramus with P_4(br.)–M_3 . . . . (W+) 72226

B′. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM W. SIDE OF SHEEP MT.:

SKULL AND MANDIBLE (ATTACHED) F:A.M.

Anterior portion of skull with P^1–M^3 and partial mandible with P_1(br.)–M_3. . . . (W) 45358

[1] In divide area between the White River and Bad River drainages, near the line between Pennington and Jackson counties.

C. FROM "CHEYENNE RIVER,"[1] SOUTH DAKOTA, 1894

2 SKULLS AND MANDIBLES		A.M.
Partial skull with P^2–M^3 and partial mandible (attached) with I_3–P_1 rt. and P_2–M_3	(w+)	1298
Partial skull with I^1–M^3 and partial mandible with /C–P_1 rt. and P_2–M_3	(w‡)	1301

The A.M. catalogue gives the horizon of the above two specimens as "upper Oreodon beds." The bullae and measurements, however, compare with those of this species from "middle Oreodon" = "Zone B" of the Brule.

D. FROM CHEYENNE RIVER DRAINAGE, U.N.S.M. COLL. LOC. SX-6, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

MAXILLAE AND MANDIBLE		U.N.S.M.
Partial left and right maxillae with P^3(br.)–M^3 and partial mandible with P_3(rt.)–M_3	(w)	28624

E. TENTATIVELY REFERRED FROM 13 MI. S. AND 7 MI. W. OF DICKINSON, STARK COUNTY, NORTH DAKOTA

MANDIBULAR RAMUS		F:A.M.
Partial right ramus with P_3(alv.)–M_2(rt.) (M_1 br.)	(w+)	49745

The above specimen is not complete enough for definite identification but is of importance owing to its geographic occurrence. Morris F. Skinner placed this specimen in "Unit No. 5" of his published section (1951, p. 58).

2. Genetochoerus (Osbornohyus) geygani,[2] new species

From oreodont faunal "Zone C" of the Brule Formation, Shannon County, South Dakota; referred remains from Shannon, Jackson, and Washabaugh counties, South Dakota; tentatively referred from Shannon County, South Dakota; and Stark County, North Dakota

DESCRIPTION

SKULL: Larger in size on an average than examples of *G.* (*O.*) *norbeckensis*; posterior portion of sagittal crest higher than in that species; nasal with acute posterior border, more so than in examples of *G.* (*O.*) *chamberlaini* (from "Zone C" of the Brule); nasal-maxilla contact above posterior border of C/; orbit looking slightly more forward than examples of *G.* (*O.*) *norbeckensis*; malar with sharper outward curve from face and tendency for more depth below orbit than last-mentioned species; infraorbital foramen in area above mid P^3; lacrimal fossa large and deep, larger but shallower and with anterior border more defined than in *G.* (*O.*) *norbeckensis*; bulla large, with slight depression or groove for hyoid, more inflated and with less prominent hyoidal groove than in examples of last-mentioned species.

MANDIBLE: Larger and more robust than examples of *G.* (*O.*) *norbeckensis*; symphysis deeper than in latter species; postsymphysis below anterior portion of P_4; pronounced apophysis developed posterior to and below condyle, more noticeable and more robust than in examples of *G. periculorum.*

DENTITION: Series longer and more robust than in examples of *G. periculorum*; C/ and P_1 larger than in mentioned species; P_2 usually crowded and set obliquely to alveolar border; P^1–P^3 each with moderately weak anterior intermediate crests.

LIMBS: Indications of being heavier than examples of *G.* (*O.*) *norbeckensis.* (Known only from fragmentary material.)

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

ILLUSTRATIONS: Figures 14–16, 19–23.

DISCUSSION

Remains of *Genetochoerus* (*Osbornohyus*)

[1] Exact collecting locality not known to writers.

[2] Named in honor of Paul Geygan, who helped to prepare some of the Frick Laboratory oreodont collection.

geygani ("Zone C" of the Brule) are intermediate in size between examples of *G.* (*O.*) *chamberlaini* ("Zone D") and those of *G.* (*O.*) *norbeckensis* ("Zone B"). The bullae of *G.* (*O.*) *geygani* are also intermediate in size and shape between those of *G.* (*O.*) *norbeckensis* and *G.* (*O.*) *chamberlaini*. The fragmentary limb remains of *G.* (*O.*) *geygani* suggest limbs with wider proximal ends than those of *M.* (*O.*) *norbeckensis*.

The F:A.M. specimens referred to this species were collected by Morris F. Skinner and associates, 1938, 1944, 1945, 1950.

Twenty-five specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, mandible with I_1–M_3, partial humerus, partial radius, partial femur, 2 partial tibiae, astragalus, and metapodial fragments. (w+) — F:A.M. 49734 — From oreodont faunal "Zone C" of Brule Formation, "35′ below *Leptauchenia*-like nodules," White River drainage, 5 mi. NW. of Slim Butte, Shannon County, South Dakota; collected by Ove Kaisen, Morris F. Skinner, and Morris F. Skinner, Jr., 1944

Figures 14–16, 20, 22, 23

A fragmentary mandibular ramus of a second individual is included in the above number. However, the skeletal elements are here considered as belonging to the same individual as the skull.

REFERRED FROM (A) SHANNON, (B) JACKSON, AND (C) WASHABAUGH COUNTIES, SOUTH DAKOTA; AND TENTATIVELY REFERRED FROM (D) SHANNON COUNTY, SOUTH DAKOTA; AND (E) STARK COUNTY, NORTH DAKOTA

A. FROM WHITE RIVER DRAINAGE, 5 MILES NORTHWEST OF SLIM BUTTE, SHANNON COUNTY, SOUTH DAKOTA

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Crushed skull with C/–M^3, mandible with I_2–M_3, partial scapula, 2 partial humeri, 2 partial radii, 2 partial ulnae, partial tibia, 5 phalanges, and vertebrae. Figure 19 (in part)	(w)	F:A.M. 49789

2 SKULLS AND MANDIBLES

Partial skull with I^1–dP^3–M^3(germ) and mandible (attached) with I_1–dP_3–M_3(germ)	(I)	49751
Partial skull with C/–P^2 rt. and dP^3–M^3(germ) and partial mandible with M_1–M_3 (germ)	(I)	49793

SKULL

Skull with I^2–M^3	(w)	49752

B. FROM DIVIDE AREA BETWEEN WHITE RIVER AND BAD RIVER DRAINAGES, JACKSON COUNTY, SOUTH DAKOTA

FROM $\frac{1}{4}$–$\frac{1}{2}$ MI. W. OF TOP OF CEDAR PASS:

2 ASSOCIATED INDIVIDUALS, IMMATURE

Partial skull with I^2–C/ br. and P^1–dP^2–M^2 and mandible (attached) with P_1–dP_2–M_2	(I)	F:A.M. 72319A
Partial right maxilla with dP^3–M^2 and partial right ramus with dP_3–M_2	(I)	72319B
Fragmentary limb elements		72319A–B

3 SKULLS AND MANDIBLES

Left anterior portion of skull with C/(rt.)–M^3(br.) (P^1–M^1 br.) and partial mandible with P_2–M_3 (P_3 rt. and M_1–M_2 br.)	(w‡)	49746
Partial right maxilla with M^1–M^3 and mandible with I_1(rt.)–M_3 (P_1 rt.)	(M+)	49747
Partial skull with C/(rt.)–M^3 and partial mandible with P_2–P_3 and M_1–M_3(br.)	(M+)	49749

FROM 1 MI. E. OF NORBECK PASS[1]:

2 SKULLS AND MANDIBLES, IMMATURE

		F:A.M.
Posterior portion of skull, partial mandible with dP_3–M_3(germ), and partial tibia	(I)	49748
Inferior portion of skull with P^1–dP^2–M^2 and partial mandible with $/C$–dP_3–M_1 .	(I)	49750

C. FROM WHITE RIVER DRAINAGE, QUIVER HILL, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL, MANDIBLE, AND ULNA

		F:A.M.
Partial skull with $C/$–P^1 rt. and P^2–M^3, mandible with I_1–I_2 alv. and I_3–M_3 (P_1 br.), and ulna	(M+)	49737

D. TENTATIVELY REFERRED FROM CHEYENNE RIVER DRAINAGE, SHEEP MOUNTAIN, NORTH OF SCHOOL OF MINES CANYON, SHANNON COUNTY, SOUTH DAKOTA

SKULL

		F:A.M.
Partial skull with $C/$–P^2 rt. and P^3(br.)–M^3	(W+)	45280

Postglenoid process with almost straight external border.

D′. TENTATIVELY REFERRED FROM WHITE RIVER DRAINAGE, ABOUT 5 MILES EAST OF ROCKY FORD BRIDGE

SKULL

		F:A.M.
Partial skull with $C/$–P^2 rt. and P^3–M^3	(W)	45281

The above specimen was collected by Ralph Mefferd and Morris Skinner, 1938. The field data indicate that the specimen was possibly from the "Upper *Oreodon* Zone" (="Zone C" of the Brule). It differs from typical examples of *G.* (*O.*) *geygani* in having more rounded and inflated bullae, approximately equal to those of *G.* (*O.*) *chamberlaini* from "Zone C," but the hyoidal groove approximates that of *G.* (*O.*) *norbeckensis* from "Zone B." In addition, the dentition is lighter than in average examples of *G.* (*O.*) *geygani.*

The contact of the premolar region with the posterior portion of the skull is in question. If the contact is correct, the premolar region would be exceptionally short.

E. TENTATIVELY REFERRED FROM LEO FITTERER'S RANCH, 13 MILES SOUTH AND 7 TO 8 MILES WEST OF DICKINSON, STARK COUNTY, NORTH DAKOTA

4 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with I^1–M^3, mandible with I_1–M_3 and partial atlas	(M+)	49736
Partial premaxilla with I^1–I^3, partial skull with P^1–M^3, partial left ramus with P_2–M_2 (M_1 br.), partial femur, and partial tibia. Figure 21	(W+)	49755
Skull with I^1(br.)–M^3 and mandible with I_1(br.)–M_3	(W+)	49758
Partial femur and partial tibia, partial scapula, partial humerus, partial radius, 2 partial tibiae, and partial pelvis.		49755 and 49758
The above limbs may belong to either of the two skulls, F:A.M. 49755 or 49758.		
Fragmentary skull with $C/$–dP^2–M^2, partial mandible with P_1–dP_2–M_2, partial tibia, and astragalus	(I)	49757

SKULL AND SKELETAL ELEMENTS

Posterior portion of skull, fragments of left maxilla with P^1(br.)–P^2(alv.) and M^1, partial humerus, vertebrae, and fragments	(M+)	49756

[1] Near Jackson and Pennington county line.

MAXILLA		F:A.M.
Partial right maxilla with M^3	(w‡)	49744
MANDIBULAR RAMUS		
Partial left ramus with I_2–dP_4–M_3(br.) (/C absent)	(I)	49721

The above specimens are here considered as occurring in deposits equal in age to those of "Zone C" of the Brule found in South Dakota, Nebraska, and Wyoming. The specimens that are complete enough for comparison differ from the type of *G.* (*O.*) *dickinsonensis* in having smaller auditory bullae and heavier dentition. These same specimens, however, also differ somewhat from examples of *G.* (*O.*) *geygani* in having slightly longer skulls, especially noticeable in the anterior portion. Perhaps the North Dakota specimens represent a geographic variety.

The fragmentary limb elements associated with these tentatively referred specimens are more massive than those referable to either *G.* (*O.*) *geygani* or *G.* (*O.*) *dickinsonensis.* These remains occurred in the zone cited by Morris F. Skinner[1] as "Unit No. 6."

3. Genetochoerus (Osbornohyus) chamberlaini,[2] new species

From oreodont faunal "Zone D" of the Brule Formation, Morrill County, Nebraska; referred remains from Sioux County, Nebraska; Shannon, Jackson, and Washabaugh counties, South Dakota; and tentatively referred from Shannon County, South Dakota

Description

Skull: Approximately equal in size to examples of *G.* (*O.*) *dickinsonensis,* but larger than examples of other species of subgenus; supraoccipital wings more widely spread than in other species of subgenus; sagittal crest higher than in other forms of phyla; nasals approaching those of *G.* (*O.*) *geygani,* posterior border less acute than in *G.* (*O.*) *dickinsonensis;* nasal-maxilla contact above posterior portion of C/; anterior nasal opening with more abrupt rise than in examples of *G.* (*O.*) *geygani;* malar similar to examples of *G.* (*O.*) *geygani;* lacrimal fossa equal in area but shallower than in latter species; paroccipital process similar to that in *G.* (*O.*) *geygani,* slightly wider at base than in *G.* (*O.*) *dickinsonensis;* bulla bulbous, well inflated, lacking hyoidal groove.

Mandible: Postsymphysis below P_4; ascending ramus slightly higher than in examples of *G.* (*O.*) *geygani.*

Dentition: Within size range of and characters similar to those of examples of *G.* (*O.*) *geygani* (holotype contains two anterior crests on P^3).

Limbs: Apparently similar to examples of *G.* (*O.*) *geygani;* more massive than those of *G.* (*O.*) *dickinsonensis.* (Known only from fragmentary material.)

Measurements: Table 6 (p. 144).

Illustrations: Figures 14–16.

Discussion

The skulls of *G.* (*O.*) *chamberlaini* ("Zone D" of the Brule) average longer than examples of *G.* (*O.*) *geygani* ("Zone C"), but the dental series are within the size range. The bullae are well inflated, and the hyoidal grooves are nearly absent. In all phyla of the oreodonts in which the bullae are inflated, the degree of inflation increases in the geologic sequence. As the greater inflation becomes apparent, the hyoidal groove becomes less prominent, until in "Zone D" of the Brule it is nearly absent to absent from all forms.

The dentition of *G.* (*O.*) *chamberlaini* is somewhat heavier and the limbs are more massive than in examples of *G.* (*O.*) *dickinsonensis,* both species here considered as coming from "Zone D" of the Brule. Additional material of both forms may indicate that *chamberlaini* is a variant or subspecies of *G.* (*O.*) *dickinsonensis.* The material at hand indicates that there are two separate forms, with *G.* (*O.*) *dickinsonensis* having some characters closer to those of *G.* (*O.*) *geygani* than to those of

[1] 1951, p. 58.

[2] Named in honor of Will Chamberlain who has aided the Frick Laboratory and other institutions in the collecting of fossil mammals in the Clarendon area of Texas.

G. (*O.*) *chamberlaini*. Perhaps more than one phylum is represented.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1938–1940, 1944, 1945.

Seventeen specimens are here recorded:

HOLOTYPE

Partial skull with C/(rt.)–M^3 (P^1 br.) and partial mandible with P_1–P_4 br. and M_1–M_3. (w‡)	U.N.S.M. 28340	From oreodont faunal "Zone D" of Brule Formation, U.N.S.M. Coll. Loc. Mo–111, 8 mi. E. of Broadwater, North Platte River drainage, Morrill County, Nebraska; collected by S. R. Sweet, Marian and Bertrand Schultz, and associates, 1935 Figures 14–16

REFERRED FROM (A) SIOUX COUNTY, NEBRASKA; (B) SHANNON, (C) JACKSON, AND (D) WASHABAUGH COUNTIES, SOUTH DAKOTA; AND TENTATIVELY REFERRED FROM (E) SHANNON COUNTY, SOUTH DAKOTA

A. FROM WHITE RIVER DRAINAGE, JODER AREA, SIOUX COUNTY, NEBRASKA

SKULL F:A.M.

Skull with C/–M^3 . . . . (w+) 49745

B. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 5 MI. NW. OF SLIM BUTTE:

SKULL AND MANDIBLE, IMMATURE

Partial skull with C/(br.)–dP^3–M^2 (P^2 alv.) and partial mandible with P_1–dP_2–M_2 . . . . (I) F:A.M. 72081

FROM E. SIDE OF SHEEP MT.:

SKULL AND MANDIBLE

Anterior portion of skull with P^3–M^3 and partial mandible with P_4–M_3 . . . . . (w‡) 45323

FROM HEAD OF WIND CREEK[1]:

SKULL, IMMATURE

Partial skull with P^1–dP^2(br.)–M^2 . . . . (I) 72142

FROM S. AND E. OF COTTONWOOD PASS:

SKULL AND MANDIBLE

Anterior inferior portion of skull with P^3–M^3 and partial mandible with P_4–M_3 . . (w‡+) 49753

MAXILLA AND MANDIBLE, IMMATURE

Partial left maxilla with dP^2(br.)–M^2 and partial mandible with dP_4–M_2 . . . . . (I) 72143

B′. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM HEAD OF INDIAN CREEK:

SKULL F:A.M.

Partial skull with C/(br.)–M^3 (P^3 and M^1–M^3 br.) . . . . (w‡+) 49729

FROM 1–1¼ MI. S. OF COTTONWOOD PASS[2] (BIG CORRAL DRAW AREA):

2 SKULLS AND MANDIBLES

Partial skull with C/–P^1 rt. and P^2–M^3 (P^2–P^3 br.) and partial mandible with P_2(rt.)–M_3 . . . . (w‡) 49735

[1] From near Shannon and Pennington county line.
[2] This locality is in the divide area between the Cheyenne and White rivers.

Partial skull with C/–dP²–M³(germ), mandible with P_1(br.)–dP_2–M_3(germ) and partial humerus . . . . (I) F:A.M. 72320

FROM AREA BETWEEN HEADS OF BIG CORRAL DRAW AND COTTONWOOD CREEK[1]:

SKULL AND MANDIBLE

Partial skull with I^1–M^3 (C/ br.) and mandible with I_2–M_3 (I_3 alv. and P_1 br.) . . (W+) 45283

SKULL AND MANDIBLE

Partial skull with C/(erupt., br.)–dP^2–M^3(germ) and partial mandible with /C(br.)–dP_2–M_3(germ) (P_1 br.). . . . . (I) 72080

FROM BETWEEN THE HEADS OF W. BIG CORRAL DRAW AND COTTONWOOD CREEK[1]:

SKULL, MANDIBLE, AND METAPODIAL

Partial skull with C/–dP^2–M^3(germ), mandible (attached) with I_1–dP_3–M_3(germ), and partial metapodial. . . . . (I) 49738

C. FROM DIVIDE AREA BETWEEN WHITE AND BAD RIVERS, JACKSON COUNTY, SOUTH DAKOTA

FROM 1 MI. E. OF NORBECK PASS[2]:

SKULL, MANDIBLE (ATTACHED), AND SKELETAL FRAGMENTS

Partial skull with C/–P^1 and M^1–M^3(germ), partial mandible with P_1(rt.)–P_2 and M_1–M_3(germ), and limb fragments . . . . (I) F:A.M. 49739

FROM 3½–4 MI. NW. OF INTERIOR:

MANDIBULAR RAMUS, IMMATURE

Partial left ramus with P_1(rt.)–dP_3–M_2 (M_1 br.) . . . . (I) 72284

D. FROM WHITE RIVER DRAINAGE, POTATO CREEK BASIN, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

Anterior portion of skull with M^1–M^3 br. and partial mandible with dP_4–M_3(br.)(M_1-br.) . . . . (W‡) F:A.M. 72079

E. TENTATIVELY REFERRED FROM 1½ MILES SOUTH OF COTTONWOOD PASS,[3] CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

Posterior portion of skull with P^4–M^3 and partial mandible with M_2–M_3 . . . . . (M) F:A.M. 49740

The field records associated with the above specimen state "Base of *Leptauchenia* Beds?" (= "Zone D" of the Brule). The partial skull is tentatively referred to this species because of the unusual bullae which are very high and narrow. The bullae are considerably different in shape from the inflated and rounded ones of any of the species of this subgenus, and they are decidedly more inflated than those of examples of *Genetochoerus* from "Zone A" of the Brule.

4. Genetochoerus (Osbornohyus) dickinsonensis (Douglass)

From "Zone D" of the Brule Formation, Stark County, North Dakota

Eucrotaphus dickinsonensis DOUGLASS, 1907c, p. 99, pl. 22.

Eporeodon dickinsonensis (Douglass): LOOMIS, 1924b, p. 8, fig. 5 (in part). THORPE, 1937, p. 68, figs. 4, 34, pl. 4, figs. 1–3.

CHARACTERS

SKULL: Approximately same size as examples of *G.* (*O.*) *chamberlaini;* supraoccipital

[1] This locality is in the divide area between the Cheyenne and White rivers.

[2] This locality is along the Pennington and Jackson county line.

[3] This locality is in the divide area between Cheyenne River and White River drainages.

wings widely spread, similar to those of latter species; sagittal crest high, similar to that of *G.* (*O.*) *chamberlaini;* nasals moderately wide, posterior border acute; nasal-maxilla contact above posterior border of C/; anterior premaxillary surface with very abrupt rise to nasals; infraorbital foramen above P^3; lacrimal fossa large, moderately deep, slightly deeper than in examples of *G.* (*O.*) *chamberlaini;* paroccipital process slightly lighter than in last-mentioned species; bulla well inflated, with slight hyoidal groove; postglenoid process somewhat more robust anteroposteriorly than in examples of *G.* (*O.*) *chamberlaini;* posterior palate projecting for short distance posterior to M^3.

MANDIBLE: Postsymphysis below posterior portion of P_3; similar to examples of *G.* (*O.*) *chamberlaini;* inferior border of ramus with sharp downward curve posterior to M_3.

DENTITION: Series lighter than in *G.* (*O.*) *chamberlaini;* both superior and inferior series show less crowding of premolars than in latter species; P^1-P^4 each with prominent anterior intermediate crest (double on P^4).

LIMBS: Lighter than examples of *G.* (*O.*) *chamberlaini.*

MEASUREMENTS: Table 6 (p. 144).

ILLUSTRATIONS: Figures 14–16, 19, 20, 22, 52.

DISCUSSION

Douglass,[1] in a discussion of the geologic occurrence of the holotype of *G.* (*Osbornohyus*) *dickinsonensis,* stated: "The specimen was found near the top of the thick nodular beds of the Middle White River (*'Oreodon'*) horizon of the Little Bad Lands near Dickinson in North Dakota. Though not suspected at the time when the specimen was collected, it is barely possible that it may have come from the upper beds which contain remains of *Eucrotaphus major* (?). The remains were not imbedded in their original position and they may have been derived from a higher level, though the specimen is quite different from any species of *Eucrotaphus* so far found in the upper beds. It is also different from the one specimen of *Eucrotaphus bullatus?* which was found in the upper portion of the *'Oreodon'* Beds."

[1] 1907c, p. 99.

The actual geological occurrences of Douglass' type is questionable. Morris F. Skinner and party from the Frick Laboratory made a collection in the area near Dickinson, which is believed to be the general locality given by Douglass. The Frick Collection, however, does not contain an example of an oreodont that is specifically the same as the holotype of *G.* (*O.*) *dickinsonensis.* The latter collection is documented stratigraphically and is tied into a published geologic section.[2] The bullae of the holotype suggest that the specimen must have occurred in deposits equal in age at least to the highest portion of Skinner's section.

The present writers realize that they are recognizing two species, *G.* (*O.*) *chamberlaini* and *G.* (*O.*) *dickinsonensis,* within the same subgenus and probably from the same faunal zone, an undesirable course (see discussion on p. 152). Perhaps the two species, however, represent two distinct phylogenetic lines. More examples of *G.* (*O.*) *dickinsonensis* and better geologic information are needed in order to clarify the exact taxonomic status of this species.

Douglass[3] originally referred the species *dickinsonensis* to the genus *Eucrotaphus.* Much discussion has been carried on in regard to *E. jacksoni,* the genotypic species of *Eucrotaphus.* The present writers consider the holotype as being an oreodont, but not complete enough for identification. (See discussion, p. 165.) The bulla preserved in the holotype of *E. jacksoni* is decidedly smaller and more depressed than that found in *G.* (*O.*) *dickinsonensis.*

Loomis[4] and Thorpe[5] both referred *dickinsonensis* to the genus *Eporeodon.* The genotypic species, *Eporeodon occidentalis,* from the John Day deposits[6] does have a light dentition somewhat similar to that of *G.* (*O.*) *dickinsonensis,* but the bulla of the latter species is large and well rounded, whereas that of *E. occidentalis* is high and almost cone-shaped. The skulls of the two species are about the same size, but the John Day skull differs in

[2] Skinner, 1951, p. 57.
[3] 1907c, p. 99.
[4] 1924b, p. 8.
[5] 1924b, p. 222; 1937, p. 68.
[6] Schultz and Falkenbach (1949, chart 3, p. 83) considered the John Day deposits approximately equal in age to the Harrison Formation of the Great Plains. See also discussion in present report (p. 199).

being lower and possessing an exceptionally deep lacrimal fossa, wide nasals, and a peglike postglenoid process. (See figs. 14, 15, 24.)

Thorpe,[1] in commenting on *G.* (*O.*) *dickinsonensis*, noted that P^4 "has two very small anterior fossettes." There actually is a small anterior intermediate crest just posterior to the regular anterior intermediate crest, thus forming two distinct small fossettes. However, the present writers do not consider the presence of the two fossettes to be of diagnostic value. There is considerable variation within some species of oreodonts in the development and size of the crests and number of fossettes. Another unusual character is the prominent style on the external border between the second and third lobe of M^3.

Thorpe further stated: "This species is a typical member of the *Eporeodon* genus and lies within the *E. major* group. If it were not for the unusual structure of P^4, I should include this form with the subspecies of *E. major*, as a geographic variant and possibly as a geologic one as well, though there is doubt on the latter points."

Thorpe also stated that this species "is the size of that of *Merycoidodon culbertsonii*." The present writers, however, consider that *M. culbertsonii* has a larger skull and also has a small (minute) bulla. *Paramerycoidodon* (*Barbourochoerus*) *major*, on the other hand, has a larger skull, larger bulla, and decidedly more robust teeth than *G.* (*O.*) *dickinsonensis*.

One specimen is here recorded:

HOLOTYPE

Skull with I^1–I^2 rt. and I^3–M^3, mandible with I_1(br.)–M_3, partial scapula, 2 partial humeri, partial ulna, partial tibia, metapodial, and vertebrae. (M+)	C.M. 1584	From oreodont faunal "Zone D" of Brule Formation,[2] "near top of thick nodular beds," near Dickinson, Stark County, North Dakota; collected by Douglass, 1905 Figured by Douglass, 1907c, pl. 22; Thorpe, 1937, fig. 34, pl. 4, figs. 1–3 This report, figures 14–16, 19, 20, 22, 52

V. PSEUDOGENETOCHOERUS,[3] NEW GENUS

GENOTYPE: *Pseudogenetochoerus covensis*, new species.

DESCRIPTION

SKULL: Small in size, larger than examples of *Genetochoerus* (*Osbornohyus*); basal length ranging from 181 to 197 mm., widths from 108 to 135 mm.; dolichocephalic; sagittal crest moderately prominent; facial region moderately high, similar to examples of *Merycoidodon* and *G.* (*Osbornohyus*) in this respect; supraoccipital wings extended for short distance posterior to condyles, wings not widely spread [similar to those of *G.* (*Osbornohyus*)]; brain case long and narrow, slightly more inflated than examples of *G.* (*Osbornohyus*); frontals moderately broad; nasals wide, wider than those of *G.* (*Osbornohyus*), posterior border acute to obtuse; anterior nasal-maxilla contact above posterior border of C/ to anterior portion of P^1; orbits roundish and large, larger than in examples of *G.* (*Osbornohyus*), looking mostly outward, slightly forward and upward; malar shallow below orbit, deeper than in examples of *G.* (*Osbornohyus*); zygomatic arch moderately light; infraorbital foramen above posterior portion of P^3 to anterior portion of P^4; lacrimal fossa small and deep, similar to that of *G.* (*Osbornohyus*), definitely smaller and shallower than in examples of *Eporeodon*; muzzle narrow; occipital condyles light; paroccipital process light, anterior external base slightly excavated; bulla well inflated, rounded, with slight hyoidal groove but large hyoidal pit; postglenoid process massive, somewhat peg-shaped.

MANDIBLE: Light, lighter than in examples of *G.* (*Osbornohyus*), more like those of *Genetochoerus* in this respect; postsymphysis

[1] 1937, p. 69.

[2] The present writers assume that the holotype is from oreodont faunal "Zone D" of the Brule because of the stage of development of the bullae and the size and other characters of the skull.

[3] False ancestral hog, indicating likeness to examples of *Genetochoerus* (*Osbornohyus*).

below P_3; ramus shallow, shallower than those of *G.* (*Osbornohyus*), approximately equal to those of *Genetochoerus*; condyle exceptionally small (proportionately smaller than examples of *Genetochoerus*).

DENTITION: Light, series as light as but longer than examples of *G.* (*Osbornohyus*), lighter than in those of *Merycoidodon*; P^1–P^3 each usually with strong intermediate crest.

LIMBS: (The limb elements are questionably associated with dentitions of this genus).

MEASUREMENTS: Table 6 (p. 144).

ILLUSTRATIONS: Figures 16, 17, 52 (skulls, mandibles), 19–23 (limbs).

DISCUSSION

Pseudogenetochoerus remains are limited to the John Day deposits (lower Miocene) of Oregon. The genus is tentatively considered to belong to the subfamily Merycoidodontinae. The morphological characters noted above indicate that the differences between *Pseudogenetochoerus* and *Genetochoerus* (*Osbornohyus*) are not great. *Genetochoerus* (*O.*) remains are restricted to the Oligocene (middle and upper Brule Formation, oreodont faunal zones "B," "C," and "D" of the Brule). Thus there seems to have been a considerable lapse of time between the period of the apparent extinction of *G.* (*Osbornohyus*) in the Great Plains region and the first appearance of *Pseudogenetochoerus* in the Oregon area. It should be noted that no remains of either group have been found in the Gering or Monroe Creek formations or in deposits of equal age in other parts of the United States. These two lower Miocene formations are below the Harrison and above the Brule in the Great Plains and represent some 500 feet of terrestrial deposits. Both the Gering and Monroe Creek have produced large quantities of oreodont remains. Most of the phylogenetic lines represented by this material show that considerable morphological change took place during the depositional time of the sediments representing the Gering and Monroe Creek formations. The apparent similarities in characters of remains of *Genetochoerus* (*Osbornohyus*) (from the Brule) and those of *Pseudogenetochoerus* (from the John Day, approximately equal to the Harrison), pose a problem of explanation, as their occurrences are widely separated in time.

Perhaps the two phyla are not closely related but instead represent a case of parallelism. The John Day line may have been derived from the same ancestral stock as was *Genetochoerus*, but developed independently at a slower rate than did the latter genus in the Great Plains. Of course, there is no actual evidence of this hypothesis since oreodont remains have not been found in deposits earlier than the middle John Day in the Oregon region. The development may have taken place in the area, but no fossil evidence has been preserved.

On the other hand, one might come to the conclusion, because of the similarities between the two forms, and because *Pseudogenetochoerus* is only slightly more advanced than the *G.* (*Osbornohyus*) line, that the John Day deposits were earlier than the Harrison, perhaps equal in age to the Gering or (and) Monroe Creek of the Great Plains. It must be remembered, however, that other John Day oreodonts (the Merychyinae,[1] the Promerycochoerinae,[2] the Phenacocoelinae,[3] and the Desmatochoerinae[4]) appear to be at the same stage of development morphologically as closely related forms from these same subfamilies of the Great Plains area which are from the Harrison Formation or from deposits of equivalent age. (See chart 6, p. 158, for comparison of genera and species from John Day deposits and those from the Great Plains). It should also be pointed out that the leptauchenins are among the most common oreodonts from the Gering and Monroe Creek formations (or their equivalent in age) in Nebraska, Wyoming, and Montana,[5] yet not a single leptauchenin specimen has been reported from the John Day deposits. The leptauchenins also are not known from the Harrison Formation of the Great Plains. Leptauchenins do occur in the west coast region in California,[6] but in deposits which appear to be of the same age as the Gering of the Great Plains.

In the revision of the subfamily Promerycochoerinae,[7] it was stated that no remains of

[1] Schultz and Falkenbach, 1947, pp. 251, 256-257.
[2] *Idem*, 1949, pp. 102, 107, 111, 118, 121, 123, 128.
[3] *Idem*, 1950, p. 123.
[4] *Idem*, 1954, pp. 182, 185, 210, 215.
[5] The lower Miocene localities in Montana are in closer proximity to the John Day deposits than they are to those in Nebraska and Wyoming.
[6] See this report (p. 241).
[7] Schultz and Falkenbach, 1949, pp. 102, 107, 111, 118, 121, 123, 128.

Mesoreodon (which are restricted to the Gering and Monroe Creek of the Great Plains) were reported from the John Day, although examples of *Promerycochoerus* [including *P.* (*Parapromerycochoerus*) and *P.* (*Pseudopromerycochoerus*)] have been found in both the middle and upper John Day deposits. Also there appear to be size changes within the *Promerycochoerus* phylum, the smaller forms presumably from the middle John Day deposits, and the larger from the upper. It is obvious that the larger examples representing this phylum (occurring questionably in the upper John Day) were actually larger than examples of the same genus or subgenus from the Great Plains. In an earlier chart (chart 3, 1949, p. 83) the present writers postulated that the John Day deposits may include a slightly higher faunal zone than is represented in the Harrison of the Great Plains. This faunal zone definitely shows more affinities to the Harrison fauna than to that of the lower Marsland. Perhaps it represents in part the period of time between the end of the Harrison deposition and the earliest Marsland.

The oreodont phylum with the longest geologic history is the *Prodesmatochoerus-Subdesmatochoerus-Desmatochoerus* line (from early Oligocene to possibly late Miocene). In this phylum, too, the John Day species of *Desmatochoerus curvidens* is at approximately the same stage of development as the closely related form *D. curvidens gregoryi*[1] from the Harrison Formation of the Great Plains.

Size alone, of course, is not the determining factor in the identifying of a specimen, but it must always be considered an important character. Although it is often said that the dentitions of oreodonts are of little diagnostic value, the present writers have observed that in some groups the tooth characters give important clues as to the geologic age of the specimens involved. For example, the dentitions of the various forms of the Merycoidodontinae from the Oligocene usually can be recognized by the type of anterior and posterior crescents on the molars, which slant more inwardly than do those of the Miocene species. The John Day examples of both *Pseudogenetochoerus* and *Epigenetochoerus* have molars of the type characteristic of those from the Harrison of the Great Plains, even though the dentitions and skulls are approximately the same size as some of those of the Oligocene merycoidodonts. If only the size and superficial skull characters were used in the classifying of the forms, the examples of *Pseudogenetochoerus covensis* and *P. condoni* could be considered as being derived from the lower and upper Gering (or equivalents in age), respectively, and *Epigenetochoerus parvus* from the lower Brule equivalent (faunal "Zone A"). Unfortunately, the oreodont remains available to the present writers from the middle and upper John Day deposits, with few exceptions, are poorly documented geologically. Therefore, in the case of the John Day species of the Merycoidodontinae, the geologic occurrence is assumed to be middle or upper John Day in the suggested phylogenetic sequences of the species. The age of the John Day deposits has been discussed in some detail by the present

[1] Schultz and Falkenbach, 1954, chart 1, pp. 156, 183.

CHART 6

Observed Distribution of Certain Genera and Subgenera in the John Day and Harrison Formations

	Oregon (John Day)	Great Plains (Harrison)
Merychyinae		
Oreodontoides	x	?x
O. (*Paroreodon*)	x	—
Promerycocherinae		
Promerycochoerus	x	x
P. (*Parapromerycochoerus*)	x	x
P. (*Pseudopromerycochoerus*)	x	x
Phenacocoelinae		
Hysiops	x	x
Desmatochoerinae		
Desmatochoerus	x	x
Pseudodesmatochoerus	x	x
Superdesmatochoerus	x	—
Merycoidodontinae[a]		
Pseudogenetochoerus	x	—
Epigenetochoerus	x	—
Eporeodontinae		
Eporeodon	x	—
E. (*Paraeporeodon*)	x	—
Dayohyus	x	—

[a] The two genera are tentatively referred to this subfamily.

writers.[1] Neither of these workers has visited the John Day deposits, but the information used by them in the various reports has been derived from the published literature and from personal conversations with those who have collected fossils and (or) studied the geology of the region. (See p. 199 for further discussion.)

The proposed sequence of the species of *Pseudogenetochoerus* is as follows: *P. condoni* from ?middle John Day, and *P. covensis* from ?upper John Day.

Distribution

Two species of *Pseudogenetochoerus* are known from Oregon. (See geologic distribution, p. 22.)

Summary of Species and Types

Two species of *Pseudogenetochoerus* from one Miocene (= Harrison Formation) locality are here recorded:

1. *Pseudogenetochoerus condoni* (Thorpe), from John Day Valley, Oregon. (?Middle John Day = approximate Harrison equivalent.)

HOLOTYPE: Skull, Y.P.M. 11016.

2. *Pseudogenetochoerus covensis,* new species, from John Day Valley, Oregon. (?Upper John Day = approximate Harrison equivalent.)

HOLOTYPE: Skull, A.M. 7509. Figures 16, 17, 19–23.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PSEUDOGENETOCHOERUS

TOTAL AVAILABLE SPECIMENS: 44

1. Pseudogenetochoerus condoni (Thorpe)

From questionably middle John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eporeodon condoni THORPE, 1921c, p. 104, figs. 6–8; 1937, p. 66, figs. 31–33.

Characters

SKULL: Slightly larger than largest examples of *Genetochoerus,* smaller than skulls of *Pseudogenetochoerus covensis*; bulla slightly smaller and hyoidal groove more prominent than in bullae of *P. covensis*; postglenoid process less massive than in *P. covensis*; shorter distance between posterior border of M^3 and the occipital condyle than in examples of *P. covensis*; palate with less posterior projection than in *P. covensis.* (See generic description.)

MANDIBLE: Smaller than examples of *P. covensis.* (See generic description.)

DENTITION: Series length within the individual variation found in examples of *P. covensis,* series longer in proportion to the skull length than those of *P. covensis.*

LIMBS: (See generic discussion).

MEASUREMENTS: Table 6 (p. 144).

ILLUSTRATIONS: Figures 16, 17, 52.

[1] 1949, p. 89, chart 3 (p. 83); this report (pp. 199 and 402).

Discussion

Pseudogenetochoerus condoni (Thorpe) was among the host of species referred to the genus *Eporeodon.* The genotypic species, *Eporeodon occidentalis,* was based on a specimen from the John Day, which is a smaller skull than examples of *P. condoni.*

Thorpe[2] listed 14 species and five subspecies under the genus *Eporeodon,* eight of these forms from the John Day deposits. (See p. 193 for reclassification in this report.) The 14 species and five subspecies ranged from Oligocene to lower Miocene. Some skulls, such as those of *Paramerycoidodon* (*Barbourochoerus*) *major,* are much larger and more robust than those of *E. occidentalis.* It has been noted in other subfamilies of oreodonts that skulls representing different species within a phylogenetic line show no increase in size from the older through the younger geological deposits. The exception to the foregoing is in the Sheep Creek-Lower Snake Creek examples of *Brachycrus,* where the later-occurring form (Lower Snake Creek) is the smallest. *Brachycrus* remains in other areas show the usual trend from small to large. There is no evidence for a case in which a phylum evolved from small to large and then became smaller and still later became larger again. Such a situation would have had to occur in the *Eporeodon* phylum, if the line were present in Oligocene as well as Miocene times.

The *Eporeodon* phylum is here recognized only from the middle (smaller-sized skull) and

[2] 1937, p. x.

the upper (larger skull) John Day. The genus is unique in the shape of the bulla, robust skull, comparatively light teeth, and very large lacrimal fossa. There are no forms in the Great Plains that are similar regardless of geologic occurrence. (See pp. 194, 199, and 402 for discussion of John Day forms and geologic occurrences).

Twenty specimens are here recorded:

HOLOTYPE

Skull with I^2–I^3 rt. and C/(br.)–M^3 (P^1 br.). (w) Y.P.M. 11016 From ?middle John Day, Bridge Creek, John Day Valley, Oregon; collected by L. S. Davis, 1874

Figured by Thorpe, 1921C, figs. 6–8; 1937, figs. 31–33

REFERRED FROM JOHN DAY AREA, OREGON

FROM ALAMO RANCH:

SKULL — A.M.

Posterior portion of skull with M^1(br.)–M^3 . . . . (w) 7735

FROM ?CAMP CREEK, CROOKED RIVER (?COLLECTED BY J. L. WORTMAN, 1879):

SKULL, MANDIBLE (ATTACHED), AND TIBIA

Anterior portion of skull with I^1–M^3(br.), partial mandible with I_1(rt.)–M_3, and partial tibia. Figure 16 (in part) . . . . (w+) 7582

A fragment of left ramus with P_4 of a second individual is included in the above number.

SKULL AND MANDIBULAR RAMUS

Posterior portion of skull and left mandibular ramus with M_1(br.)–M_3(br.) . . . (w‡) 7818

SKULL

Anterior portion of skull with I^1–I^3 alv. and C/(rt.)–M^3 (P^1–P^2 rt.). Figure 52 (in part) . . . . (w) 7881

MANDIBULAR RAMI

Partial right ramus with dP_3(br.)–M_1 . . . . (I) 7831

Partial mandible with P_3–M_3 . . . . (w+) 7832

The above two specimens were found associated in the field.

FROM THE "COVE":

2 SKULLS

Partial skull with C/(rt.)–M^3 (P^1–M^1 br.) . . . . (w+) 7511

Above collected by C. H. Sternberg, 1878.

Partial skull with C/–M^3 . . . . (w‡‡) 7669

Above collected by William Day, 1878.

The canine of above specimen is exceptionally massive.

FROM U.C. COLL. LOC. NO. 818 (COLLECTED BY J. B. REINSTEIN, 1899):

SKULL AND ATLAS (ATTACHED) — U.C.

Partial skull with I^1–M^3 and atlas . . . . (w+) 94

FROM U.C. COLL. LOC. NO. 898 (COLLECTED BY DAVIS AND OSMONT, 1900):

SKULL, MANDIBLE, ATLAS, AND AXIS (ATTACHED)

Skull with I^1–M^3, mandible with I_1–M_3, atlas, and axis 1910

FROM C.I.T. COLL. LOC. NO. 136 (COLLECTED BY GAZIN AND HASTINGS, 1938):

SKULL — C.I.T.

Anterior portion of skull with C/–P^2 rt. and P^3–M^3(br.) . . . . (w‡+) 512

FROM GENERAL AREA:

SKULL AND MANDIBLE (ATTACHED)		A.M.
Anterior portion of skull with I^3–M^3 and partial mandible with I_1–M_3	(w)	7559
6 SKULLS		
Skull with I^1–I^3 rt. and P^1–M^3. Figure 17	(w‡)	7498
The above specimen seems to be the skull referred to *Eucrotaphus jacksoni* by Cope, 1884b, p. 518.		
Partial skull with I^2–M^3	(w‡)	7523
Included under the same catalogue number are fragmentary skeletal elements that seem to be too small for the size of the skull. They are more the size of limbs expected to be found with *Oreodontoides* or *O.* (*Paraoreodon*).		
Posterior portion of skull with P^4–M^1 rt. and pelvic fragments		7563
Anterior portion of skull with C/(rt.)–M^3(br.) (P^1–M^2 br.)	(w‡+)	7573
Skull with C/–M^3	(M+)	7657
Included under the above catalogue number are fragmentary limb elements of two forms of different sizes, perhaps *Oreodontoides* and *Promerycochoerus;* also a specimen with this number listed under *E.* (*Paraeporeodon*) *longifrons*.		U.O.
Partial skull with I^1–P^1 rt. and P^2–M^3 (P^4 rt.).	(M+)	F677
Bulla larger than in holotype.		

FROM "PROBABLY HAY STACK VALLEY":

SKULL		Y.P.M.
Partial skull with C/–M^3 (P^2–P^3 alv.)	(w‡)	11029
Per Thorpe (1937, p. 66), paratype of *P. condoni*.		

2. **Pseudogenetochoerus covensis,**[1] new species

From questionably upper[2] John Day
(approximately equal in age to the
Harrison of the Great Plains),
John Day Valley, Oregon

DESCRIPTION

SKULL: Larger than in examples of *P. condoni*; bulla larger, hyoidal groove less prominent than in examples of *P. condoni*; postglenoid process bulbous, more massive than those of *P. condoni*; greater distance between posterior border of M^3 and occipital condyle than in examples of *P. condoni*; posterior palate extended posteriorly for considerable distance (10 mm. plus or minus), greater distance than in *P. condoni.*

MANDIBLE: Larger than in examples of *P. condoni.* (See generic description.)

DENTITION: Series length within variation found in examples of *P. condoni,* shorter in proportion to length of skull than in that species.

LIMBS: (See generic discussion).

[1] Named after the "Cove," a collecting area in the John Day Valley of Oregon.

[2] See discussion of middle and upper John Day on page 194.

MEASUREMENTS: Table 6 (p. 144).

ILLUSTRATIONS: Figures 16, 17, 19–23, 52.

DISCUSSION

The questionable occurrence of the John Day oreodonts is discussed on page 199. It is definitely stated that the writers have no knowledge of the geologic occurrence of most of the John Day collections. Thorpe used the color of the matrix adhering to the skulls as a key to the particular part of the beds from which the specimen came. The fallacy of Thorpe's method is discussed on page 199.

There seems to be complete agreement among persons who have collected in the John Day area that there are three divisions: the lowest, which contains no fossil mammals, and the middle and upper portions. The collections seem to indicate, however, that there is not always agreement in what constitutes the middle and upper John Day.[3]

The morphologic characters of the various forms occurring in the John Day deposits do suggest a possible geologic sequence, but there is no evidence to substantiate this possibility.

Twenty-five specimens are here recorded:

[3] See Schultz and Falkenbach, 1949, p. 89.

HOLOTYPE

Skull with I^1–M^3 and mandible with I_1–M_3. (w‡)	A.M. 7509	From the "Cove," John Day Valley, Oregon; collected by Day and Warfield, 1877 Figures 16, 17, 19–23

The following 4 mandibular rami and skeletal elements were all given the same catalogue number as the holotype. The 1 through 5 numbers were affixed to the catalogue number in order to differentiate the various specimens under the number. All collected by Day and Warfield, 1877.

REFERRED FROM JOHN DAY VALLEY, OREGON

FROM THE "COVE" (=TURTLE COVE):

4 MANDIBULAR RAMI AND SKELETAL ELEMENTS		A.M.
Partial mandible with I_1(alv.)–M_3 (I_2–P_2 rt. and P_4 br.)	(w‡)	7509–(1)
Partial mandible with I_1–/C rt. and P_1–dP_4–M_3 (P_2 rt.)	(I)	7509–(2)
Partial right ramus with /C–P_1 alv. and P_2(rt.)–M_3 (P_3 br.)	(w+)	7509–(3)
Partial right ramus with P_4–M_3(br.)	(w+)	7509–(4)
The P_4 of the above ramus is large for this species.		
2 partial scapulae, partial humerus, 2 partial radii, partial ulna, partial femur, partial tibia, astragalus, calcaneum, and metapodials		7509–(5)
The above limb elements may belong to the holotype. The *Promerycochoerus*-like limb fragments under the same catalogue numbers, A.M. 7509, are not listed.		

2 SKULLS		
4 sections of skull with I^3–P^3 rt. and M^1(br.)–M^3	(w+)	7540
The above collected by C. H. Sternberg, 1878.		
Partial skull with I^1–I^3 alv. and C/–M^3 (P^1 br.) (small bulla)	(w‡)	7659
The above collected by Day and Warfield, 1877.		

FROM TURTLE COVE (COLLECTED BY L. S. DAVIS, 1879):

SKULL		
Partial skull with C/(rt.)–M^3	(w+)	7611

FROM CAMP CREEK, CROOKED RIVER (COLLECTED BY J. L. WORTMAN, 1877):

SKULL, IMMATURE		
Skull with I^1–I^3 rt. and C/–dP^2 br. and dP^3–M^3	(I)	7564

MANDIBULAR RAMUS		
Partial right ramus with P^3–M^3	(w‡+)	7652
A humerus and partial tibia included under above number are referable to *Promerycochoerus*.		

FROM C.I.T. COLL. LOC. NO. 210:

SKULL AND MANDIBLE (ATTACHED)		C.I.T.
Skull with C/–M^3 and mandible with I_1–M_3	(w+)	2694

FROM C.I.T. COLL. LOC. NO. 247:

SKULL		
Partial skull with C/–M^3. Figure 52 (in part)	(M+)	2688

FROM C.I.T. COLL. LOC. NO. 4:

SKULL		
Partial skull with I^2–I^3 rt. and C/–M^3	(w‡+)	538

FROM C.I.T. COLL. LOC. NO. 136 (COLLECTED BY GAZIN AND HASTINGS, 1928):

SKULL AND MANDIBLE		C.I.T.
Anterior portion of skull with I^1–P^2 rt. and P^3–M^3	(W)	513

FROM U.C. COLL. LOC. NO. 810 (COLLECTED BY CAIKINS, 1899):

SKULL		U.C.
Crushed partial skull with I^3–P^3 rt. and P^4(br.)–M^3(br.)	(W+)	130

FROM U.C. COLL. LOC. 834 (1899):

SKULL		
Partial skull with C/(rt.)–M^3 (P^1 rt., P^2 br., P^3 rt., and M^2 br.)	(M)	383

FROM U.C. COLL. LOC. NO. 898 (COLLECTED BY DAVIS AND OSMONT, 1900):

SKULL		
Partial skull with I^1–I^3 alv. and C/–M^3	(W)	2169

FROM U.C. COLL. LOC. NO. 906 (COLLECTED BY DAVIS AND OSMONT, 1900):

SKULL		
Partial skull with P^1(rt.)–M^3	(W‡$^+$)	2255

FROM NORTH FORK (CONDON COLLECTION):

SKULL, MANDIBLE (ATTACHED), AND SKELETAL FRAGMENTS		U.O.
Skull, mandible, and skeletal fragments		695
SKULL AND SKELETAL ELEMENTS		
Partial skull with C/(rt.)–M^3, partial humerus, partial radius, and foot bones	(W‡)	1049

FROM GENERAL AREA:

3 SKULLS		A.M.
Skull with C/–dP^2–M^3(erupt.)	(I)	7621
The above collected by C. H. Sternberg, 1879. A fragmentary left ramus with P_3(rt.)–M_1 included under above number is about the size of that of *O.* (*Paroreodon*) *stocki.*		
Anterior portion of skull with I^1–M^1(br.)	(W‡)	7554
Anterior portion of skull with C/–P^2 rt. and P^3–M^3	(M+)	7834
MANDIBULAR RAMUS AND HUMERUS		
Partial left ramus with P_3–M_3, and humerus	(W+)	7558

VI. EPIGENETOCHOERUS,[1] NEW GENUS

GENOTYPE: *Epigenetochoerus parvus* (Thorpe).

DESCRIPTION

SKULL: Small in size, approximate size of examples of *Genetochoerus*; basal length, 160 mm., width, 105 mm.; dolichocephalic; supraoccipital wings and sagittal crest damaged but suggesting similarity to examples of *Genetochoerus*; brain case long and narrow; frontals moderately broad; nasals light; orbits of medium size, roundish; malar light below orbit, considerable variation in depth (perhaps sex variation); zygomatic arch broken, suggesting lightness; infraorbital foramen above P^3; lacrimal fossa small but moderately deep, decidedly smaller than in examples of *Genetochoerus*; muzzle narrow; occipital condyle light; paroccipital process light, anterior external surface slightly excavated; bulla well inflated, not so large proportionately as bullae of *G.* (*Osbornohyus*) *chamberlaini* from "Zone D" of Brule, more laterally compressed and longer anteroposteriorly than in that form; postglenoid process robust; posterior palate

[1] Above *Genetochoerus*.

projecting posteriorly for considerable distance posterior to M^3, more so than in other examples of the Merycoidondontinae.

MANDIBLE: Light, postsymphysis below anterior portion of P^4; ramus shallow, deeper than in examples of *Genetochoerus*; condyle small.

DENTITION: Light, lighter than in examples of *G.* (*Osbornohyus*); P^1–P^3 each with weak anterior intermediate crest; premolar series shorter and lighter than examples of *Genetochoerus or G.* (*Osbornohyus*).

LIMBS: Moderately short and light, same length but slightly more robust than examples of *Genetochoerus periculorum.*

MEASUREMENTS: Table 6 (p. 144).

ILLUSTRATIONS: Figures 18, 52 (skull, mandible, and dentition), 19–23 (limbs).

DISCUSSION

Epigenetochoerus is questionably included under the subfamily Merycoidodontinae. In many respects the genus is like *Pseudogenetochoerus,* in that both have some characters that are similar to those of the Merycoidodontinae. Perhaps some characters are closer to those found in *Genetochoerus* and *G.* (*Osbornohyus*). Parallelism or independent development in the Oregon area may be represented.

The present writers believe that the John Day deposits are approximately equal to the Harrison of the Great Plains (see p. 194).

The new genus *Epigenetochoerus* is based on one species only, but it is definitely different from any other genera known from the John Day. Remains of *E. parvus* in some respects suggest a dwarf form of the Desmatochoerinae.

DISTRIBUTION

One species of *Epigenetochoerus* is known from the lower Miocene (=Harrison in part) of Oregon. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

One species of *Epigenetochoerus* from one lower Miocene locality is here recorded:

1. *Epigenetochoerus parvus* (Thorpe), from John Day Valley, Oregon. (John Day = approximately Harrison equivalent in age.)

HOLOTYPE: Skull, mandible, and skeletal elements, Y.P.M. 12425.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

EPIGENETOCHOERUS

TOTAL AVAILABLE SPECIMENS: 5

1. Epigenetochoerus parvus (Thorpe)

From John Day deposits (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eporeodon trigonocephalus parvus THORPE, 1921c, p. 101.

Eporeodon parvus THORPE, 1937, p. 84, figs. 44–45.

CHARACTERS

SKULL: Small, equal in size to smallest examples of subfamily, *Genetochoerus periculorum.* (See generic characters.)

MANDIBLE: (See generic characters).

DENTITION: (See generic characters).

LIMBS: (See generic description).

MEASUREMENTS: Tables 6 and 7 (pp. 144 and 146).

ILLUSTRATIONS: Figures 18–23, 52.

DISCUSSION

Examples of *Epigenetochoerus parvus* are the only ones referable to this genus; hence the generic and the specific description is the same. The skull in size is approximately equal to the larger examples of the Merychyinae from the John Day area, but in general contour is more like that of a dwarf form of the Desmatochoerinae.

The teeth are light, more like those of *Genetochoerus,* but much lighter than are found in the Desmatochoerinae. The auditory bulla is laterally compressed and long anteroposteriorly (similar to average in the Desmatochoerinae) with a deep hyoidal pit similar to that in *Pseudogenetochoerus.*

Specimen Y.P.M. 12420 is figured in this report, as it is more complete than the holotype. This specimen was not cited by Thorpe in 1937.

Thorpe[1] stated the geologic horizon for the holotype and his paratype, Y.P.M. 12426, as "Upper Oligocene (middle John Day-matrix green)." The writers do not consider the color of the matrix indicative of the geologic horizon, as has been discussed throughout the oreodont reports. The examples of *P. parvus* may have occurred in either the middle or upper John Day, based on the evidence available to the present writers.

Five specimens are here recorded:

HOLOTYPE

Crushed skull with I^1–I^3 rt. and C/–M^3, mandible (attached) with I_1–/C rt. and P_1–M_3 and skeletal fragments. (w‡+)	Y.P.M. 12425	From Haystack Valley, John Day River, Oregon; collected by L. S. Davis, 1875. Figured by Thorpe, 1921c, figs. 4–5; 1937, figs. 44, 45

REFERRED FROM JOHN DAY VALLEY, OREGON

FROM HAYSTACK VALLEY (SAME AREA AS TYPE) (COLLECTED BY C. H. STERNBERG, 1878):

MANDIBLE AND SKELETAL ELEMENTS

		A.M.
Partial mandible with I_1(rt.)–M_3, 2 humeri (1 partial), 2 radii, 2 ulnae (1 partial), 2 femora, 2 tibiae, calcaneum, astragalus, partial pes, partial pelvis, vertebrae, and ribs: Figures 19–23	(w+)	7588

FROM TURTLE COVE (COLLECTED BY WILLIAM DAY, 1876):

2 SKULLS AND MANDIBLES

		Y.P.M.
Partial skull with I^1–M^3 and mandible with I_1–I_3 rt. and /C–M_3. Figures 18, 52	(M+)	12420
Anterior portion of skull with I^3(rt.)–M^3 (C/ rt.), and fragments of mandible. Paratype, Thorpe, 1937.	(w+)	12426

FROM GENERAL AREA:

SKULL

		A.M.
Anterior portion of skull with I^1(alv.)–M^3	(w‡)	7552

The above specimen differs from the type in having the nasals retracted anteriorly for 14.5 mm.

NOMEN VANUM

"EUCROTAPHUS" LEIDY

Eucrotaphus LEIDY, 1850b, p. 90. SCOTT, 1890b, p. 320 (synonym of *Oreodon*). ZITTEL AND SCHLOSSER, 1911, p. 483 (synonym of *Eporeodon*); 1923, p. 572.

"GENOTYPE": *"Eucrotaphus jacksoni"* Leidy.

"Eucrotaphus jacksoni" Leidy

From the vicinity of Fort Laramie,
North Platte Valley, Wyoming

Eucrotaphus jacksoni LEIDY, 1850b, p. 90; 1854a, pp. 56, 113, pl. 7, figs. 4–6. THORPE, 1937, p. 61, pl. 1, figs. 13–15.

Eporeodon jacksoni (Leidy): GERVAIS, 1859, p. 36.

Oreodon jacksoni (Leidy): SCOTT, 1890b, p. 372, pl. 10, fig. 2.

[1] 1937, p. 84.

DISCUSSION

The genus and species *"Eucrotaphus jacksoni"* Leidy were established on a fragmentary posterior portion of a skull, lacking dentition. Leidy's diagnostic characters of the holotype are common to several different oreodonts. The holotype may represent an immature individual. The bulla is inflated but is of small size, and the postglenoid process is squarish, but wider transversely than anteroposteriorly.

Leidy, in 1851,[2] considered *"Eucrotaphus"* a possible synonym of *"Oreodon"* (=*Merycoidodon*), but later he[3] reported, "I suspect the latter two [*Agriochoerus* and *Eucrotaphus*] are in reality the same genus." The present

[2] 1851a, p. 239.

[3] 1854a, p. 56.

writers believe that *"Eucrotaphus jacksoni"* is an oreodont and not an agriochoerid.

Thorpe[1] considered *"Eucrotaphus"* a synonym of *Eporeodon* and reported: "I realize that this is a personal opinion and that other workers may reverse my decision. At any rate, I believe either that the species now listed under *Eporeodon* should remain there or that all of them should be transferred to *Eucrotaphus,* if this genus is considered sufficiently well defined to stand alone." Thorpe also pointed out that "in the later publications of Loomis, Matthew, Osborn, Scott, and many other vertebrate paleontologists the genus *Eucrotaphus* has been almost completely abandoned in favor of *Eporeodon.*"

Simpson[2] did not include *"Eucrotaphus"* as a valid genus in his classification of the oreodonts and concluded: "As reviewed by Thorpe, there is some evidence that this genus [*Eporeodon*] is synonymous with †*Eucrotaphus* Leidy, 1850, and hence should bear the latter name. Leidy's genus [*Eucrotaphus*] is, however, practically indeterminate and his name can well be considered a *nomen vanum,* as it has in practice. The very widespread and important genus is always called †*Eporeodon,* and it would be contrary to common sense and is not unequivocally necessary under the Rules to start calling it †*Eucrotaphus* at this time."

The present writers have come to the conclusion that *Eporeodon* and *"Eucrotaphus"* are two distinct forms. In fact, when all of the available characters are considered, it is evident that the two genera represent separate subfamilies. *"Eucrotaphus jacksoni"* appears to be closely related to *Promesoreodon scanloni,*[3] but the former species has a more massive postglenoid process than the latter. The questionable form is also similar to *Otionohyus* (*Otarohyus*) *alexi,* but the latter species does possess a higher postglenoid process. Because of the fragmentary condition of the holotype of *"E. jacksoni,"* it is difficult to note sufficient characters to use for definite identification.

It is understandable that *"E. jacksoni"* can be similar to both of these forms [*P. scanloni* and *O.* (*O.*) *alexi*], since the present writers believe that the *Promesoreodon-Mesoreodon-Promerychochoerus* phylum may have been derived from the *Otionohyus-O.* (*Otarohyus*) line, possibly during medial Oligocene times. The fact that the holotype of *"E. jacksoni"* somewhat resembles both of the above species may indicate a relationship to them. However, as mentioned previously, the holotype may be an immature specimen of some other species and genus. Also it should be noted that the geologic occurrence of *"E. jacksoni"* is unknown. In view of the foregoing discussion, it is here suggested that the genus and species *"Eucrotaphus jacksoni"* be discarded and considered a *nomen vanum.*

HOLOTYPE

Fragmentary, posterior portion of cranium (lacking dentition).	A.N.S.P. 10678	"From the vicinity of Fort Laramie," on the Platte River, Wyoming; collected by "the son of Mr. Joseph Culbertson" Figured by Leidy, 1854a, pl. 7, figs. 4–6; Thorpe, 1937, pl. 1, figs. 13–15 This report, figure 11

[1] 1937, p. 62.
[2] 1945, p. 149.
[3] Schultz and Falkenbach, 1949, p. 152.

EXPLANATION OF TEXT FIGURES 1–23

FIG. 1. Lateral views of skulls: *Merycoidodon forsythae,* new species, holotype, F:A.M. 72303 (P^3 restored from opposite side), from oreodont faunal "Zone B" of Chadron Formation, Natrona County, Wyoming (see referred ramus, fig. 3); *M. culbertsonii browni,* new subspecies, holotype, F:A.M. 72286 (some restoration from opposite side), from "Zone C" of Chadron Formation, Niobrara County, Wyoming (see ramus, fig. 3); *M. culbertsonii osborni,* new subspecies, holotype, F:A.M. 49668 (I^1-I^2 from opposite side), from oreodont faunal "Zone A" of Brule Formation, Shannon County, South Dakota (see ramus, fig. 3), referred, F:A.M. 45217A and 45217B (dorsal views only in outline, skulls found associated), from "Zone A" of Brule Formation, Pennington County, South Dakota (arrows indicate variation in post-nasal border and supraorbital foramina); *M. culbertsonii* Leidy, referred, F:A.M. 45155 (some restoration from opposite side [fig. 2, P^3 from opposite side]), from "Zone A" of Brule Formation, Pennington County, South Dakota (see ramus, fig. 3); *M. macrorhinus* (Douglass), holotype, C.M. 767, from "Zone A" of Brule Formation, Broadwater County, Montana. ×½. IF, infraorbital foramen; MA, external auditory meatus; PG, postglenoid process; PP, paroccipital process; T, holotype.

FIG. 2. Dorsal and ventral views of skulls (same as fig. 1). ×½.

APF, anterior palatine foramen; B, auditory bulla; FO, foramen ovale; MA, external auditory meatus; NF, nasal-frontal contact; PG, postglenoid process; PP, paroccipital process; PPF, posterior palatine foramen; PPR, posterior palatine projection; SOF, supraorbital foramen; Z, depression for tympanohyal; 5, lacerated foramen; 6, glenoid foramen; 7, condylar foramen.

FIG. 3. Dorsal and ventral views of skulls: *Merycoidodon macrorhinus* (Douglass), (same as fig. 1).

Superior dentition: *Merycoidodon culbertsonii* Leidy, cotype, A.N.S.P. 10728, from oreodont faunal "Zone A" of Brule Formation, South Dakota. (After Leidy).

Inferior dentition and mandibular rami: *M. forsythae,* new species, referred, F:A.M. 72308, from "Zone B" of Chadron Formation, Natrona County, Wyoming; *M. c. browni,* new subspecies, holotype, F:A.M. 72286; *M. c. osborni,* new subspecies, holotype, and *M. culbertsonii* Leidy, referred (same as fig. 1); *M. culbertsonii* Leidy, cotype, A.N.S.P. 10727, from "Zone A" of Brule Formation, South Dakota (after Leidy). ×½. PS, postsymphysis.

FIG. 4. Lateral views of skulls: *Merycoidodon (Anomerycoidodon) dani,* new species, holotype, F:A.M. 72132 (P^2 from opposite side), from oreodont faunal "Zone B" of Brule Formation, Stark County, North Dakota (see ramus, fig. 6); *M. (A.) lambi,* new species, holotype, F:A.M. 72139, from "Zone D" of Brule Formation, Jackson County, South Dakota (see ramus, fig. 6); *Merycoidodon (Blickohyus) galushai,* new species, holotype, F:A.M. 45279 (C/ from opposite side), from "Zone C" of Brule Formation, Jackson County, South Dakota (see ramus, fig. 6); *M. (B.) lynchi,* new species, holotype, F:A.M. 45297 (C/-P^2 from opposite side), from "Zone D" of Brule Formation, Pennington County, South Dakota (see ramus, fig. 6).

Dorsal view of skull: *M. (A.) dani,* new species, holotype, F:A.M. 72132 (same information as above). ×½.

FIG. 5. Ventral and dorsal views of skulls (same as fig. 4 [ventral view only of F:A.M. 72132]).

Superior dentition: *M. (A.) lambi,* new species, referred, F:A.M. 72124, from oreodont faunal "Zone D" of Brule Formation, Washabaugh County, South Dakota. ×½.

FIG. 6. Inferior dentitions and mandibular rami: *Merycoidodon (Anomerycoidodon) dani,* new species, holotype, F:A.M. 72132, from oreodont faunal "Zone B" of Brule Formation, Stark County, North Dakota (see skull, figs. 4 and 5); *M. (A.) lambi,* new species, holotype, F:A.M. 72139, from "Zone D" of Brule Formation, Jackson County, South Dakota (see skull, figs. 4 and 5); *Merycoidodon (Blickohyus) galushai,* new species, holotype, F:A.M. 45279, from "Zone C" of Brule Formation, Jackson County, South Dakota (see skull, figs. 4 and 5); *M. (B.) lynchi,* new species, holotype, F:A.M. 45297, from "Zone D" of Brule Formation, Pennington County, South Dakota (see skull, figs. 4 and 5); *Paramerycoidodon georgei,* new species, referred, F:A.M. 72210 and 45157 (inferior dentition only) from "Zone A" of Brule Formation, Shannon and Pennington counties, South Dakota (see holotype skull, figs. 4 and 5); *Paramerycoidodon (Barbourochoerus) major* (Leidy), referred, F:A.M. 45298 (I_1-P_3 from opposite side), from "Zone D" of Brule Formation, Washabaugh County, South Dakota (see referred skull, figs. 7, 8, and 9, holotype, maxilla, fig. 9); *Paramerycoidodon (Gregoryochoerus) wanlessi,* new species, holotype, F:A.M. 72014, from "Zone D" of Brule Formation, Shannon County, South Dakota (see skull, figs. 7, 8, and 9); *P. (G.)*

meagherensis (Koerner), referred, F:A.M. 45462 (P_3–P_4 from opposite side), from deposits equal in age to the Gering Formation, Meagher County, Montana (see skull, figs. 7 and 9). ×½.

FIG. 7. Lateral views of skulls: *Paramerycoidodon georgei*, new species, holotype, F:A.M. 45143, from oreodont faunal "Zone A" of Brule Formation, Shannon County, South Dakota (see ramus, fig. 6); *Paramerycoidodon* (*Barbourochoerus*) *bacai*, new species, holotype, U.N.S.M. 28191 (M^3 combination of both sides), from "Zone B" of Brule Formation, Sioux County, Nebraska; *P.* (*B.*) *major* (Leidy), referred, F:A.M. 45298 (P^2 from opposite side), from "Zone D" of Brule Formation, Washabaugh County, South Dakota (see ramus, fig. 6); *P.* (*Gregoryochoerus*) *wanlessi*, new species, holotype, F:A.M. 72014 (C/ from opposite side), from "Zone A" of Brule Formation, Shannon County, South Dakota (see ramus, fig. 6); *P.* (*G.*) *meagherensis* (Koerner), referred, F:A.M. 45462 (combination of both sides), from deposits equal in age to Gering Formation, Meagher County, Montana (see ramus, fig. 6). ×½.

FIG. 8. Dorsal views of skulls [same as fig. 7, *P.* (*G.*) *meagherensis* not shown]. ×½.

FIG. 9. Ventral views of skulls (same as fig. 7). ×½.

Superior dentition: *Paramerycoidodon georgei*, new species, referred, F:A.M. 45157 (P^1 from opposite side), from oreodont faunal "Zone A" of Brule Formation, Pennington County, South Dakota; *P.* (*B.*) *bacai*, new species, referred, U.N.S.M. 28469, from "Zone B" of Brule Formation, Sioux County, Nebraska; *P.* (*Barbourochoerus*) *major* (Leidy), holotype, U.N.S.M. 19099, from "Zone D" of Brule Formation, South Dakota. ×½.

FIG. 10. Lateral, dorsal, and ventral views of skulls: *Otionohyus wardi*, new species, holotype, F:A.M. 49662 (postglenoid process from opposite side), from oreodont faunal "Zone A" of Brule Formation, Sioux County, Nebraska (see ramus, fig. 11); *O. w. degrooti*, new subspecies, holotype, F:A.M. 49760 (C/ and auditory bulla from opposite side), from "Zone C" of Chadron Formation, Converse County, Wyoming (see ramus, fig. 11); *?O. vanderpooli*, new species, holotype, F:A.M. 49766 (ventral view, combination of both sides), from "Zone C" of Chadron Formation, Sioux County, Nebraska. ×½.

FIG. 11. Inferior dentition and mandibular rami: *Otionohyus wardi*, new species, holotype (same as fig. 10); *O. w. degrooti*, new subspecies, holotype (/C restored from opposite side) (same as fig. 10); *Otionohyus* (*Otarohyus*) *bullatus* (Leidy), referred, F:A.M. 45267, from oreodont faunal "Zone B" of Brule Formation, Shannon County, South Dakota (see skull, figs. 12 and 13); *O.* (*O.*) *cedrensis* (Matthew), holotype, A.M. 8949 (dP_4 restored from opposite side, M_3 germ drawn), from ?"Zone C" of Brule Formation, Logan County, Colorado (see skull, figs. 12 and 13); *O.* (*O.*) *hybridus* (Leidy), referred, F:A.M. 72009, from "Zone C" of Brule Formation, Washabaugh County, South Dakota (see skull, figs. 11 and 12); *O.* (*O.*) *hybridus helenae* (Douglass), holotype, C.M. 765, from "Zone C" of Brule Formation, Broadwater County, Montana; *O.* (*O.*) *alexi*, new species, referred, F:A.M. 72065, from "Zone D" of Brule Formation, Washabaugh County, South Dakota (see skull, figs. 11 and 12).

Cranium: *"Eucrotaphus jacksoni"* Leidy, holotype, A.N.S.P. 10678, from Wyoming. ×½. B, auditory bulla.

FIG. 12. Lateral and dorsal views of skulls: *Otionohyus* (*Otarohyus*) *bullatus* (Leidy), referred, F:A.M. 45267 (occipital wing and P^4 restored from opposite side), from oreodont faunal "Zone B" of Brule Formation, Shannon County, South Dakota (see ramus, fig. 11); *O.* (*O.*) *cedrensis* (Matthew), holotype, A.M. 8949 (combination of both sides); from ?"Zone B" of Brule Formation, Logan County, Colorado (dorsal view absent, see ramus, fig. 11); and referred, F:A.M. 45272 (combination of both sides), from "Zone B" of Brule Formation, Weld County, Colorado.

Lateral views of skulls: *O.* (*O.*) *hybridus* (Leidy), referred, F:A.M. 72009 (glenoid surface from opposite side), from oreodont faunal "Zone C" of Brule Formation, Washabaugh County, South Dakota (see ramus, fig. 11); *O.* (*O.*) *h. helenae* (Douglass), holotype, C.M. 765 (combination of both sides), ?"Zone C" of Brule Formation, Broadwater County, Montana (see ramus, fig. 11); *O.* (*O.*) *alexi*, new species, holotype, F:A.M. 72060 (lacrimal fossa from opposite side), from "Zone D" of Brule Formation, Washabaugh County, South Dakota (see ramus, fig. 11). ×½.

FIG. 13. Dorsal and ventral views of skulls (same as fig. 12). ×½.

FIG. 14. Lateral and dorsal views of skulls: *Genetochoerus periculorum* (Cope), holotype, A.M. 6397 (C/ and glenoid surface from opposite side), from oreodont faunal "Zone A" of Brule

Formation, Logan County, Colorado (see ramus, fig. 16), referred, F:A.M. 49730 (P^1 restored from opposite side), from "Zone A" of Brule Formation, Sioux County, Nebraska (see ramus, fig. 16).

Lateral views of skulls: *G.* (*Osbornohyus*) *norbeckensis,* new species, holotype, F:A.M. 49733 (combination of both sides), from "Zone B" of Brule Formation, Jackson County, South Dakota (see ramus, fig. 16); *G.* (*O.*) *geygani,* new species, holotype, F:A.M. 49734, from "Zone C" of Brule Formation, Shannon County, South Dakota (see ramus, fig. 16); *G.* (*O.*) *chamberlaini,* new species, holotype, U.N.S.M. 28340 (combination of both sides), from "Zone D" of Brule Formation, Morrill County, Nebraska (see ramus, fig. 16); *G.* (*O.*) *dickinsonensis* (Douglass), holotype, C.M. 1584 (combination of both sides), from "Zone D" of Brule Formation, Stark County, North Dakota (see ramus, fig. 16). $\times\frac{1}{2}$.

FIG. 15. Dorsal and ventral views of skulls (same as fig. 14). $\times\frac{1}{2}$.

FIG. 16. Inferior dentition and mandibular rami: *Genetochoerus periculorum* (Cope), holotype (I_2–/C and process from opposite side), and referred, *G.* (*Osbornohyus*) *norbeckensis,* new species, holotype, *G.* (*O.*) *geygani,* new species, holotype, *G.* (*O.*) *chamberlaini,* new species, holotype, and *G.* (*O.*) *dickinsonensis* (Douglass), holotype (P_3 and process from opposite side), all as in figure 14; and *Pseudogenetochoerus condoni* (Thorpe), referred, A.M. 7582, from ?middle John Day (= approximate age of Harrison Formation), Oregon (see skull, fig. 17); *P. covensis,* new species, holotype, A.M. 7509 (I_1-I_2 from opposite side), from ?upper John Day (= approximate age of Harrison), Oregon (see skull, fig. 17). $\times\frac{1}{2}$.

FIG. 17. Lateral, dorsal, and ventral views of skulls: *Pseudogenetochoerus condoni* (Thorpe), referred, A.M. 7498 (P^1–P^2 and M^1 restored from opposite side), from ?middle John Day (= approximate age of Harrison), Oregon; *P. covensis,* new species, holotype, A.M. 7509 (P^1–P^2, M^1, bulla, and paroccipital process restored from opposite side), ?upper John Day (= approximate age of Harrison), Oregon. $\times\frac{1}{2}$.

FIG. 18. Lateral, dorsal, and ventral views of skulls, ramus, and inferior dentition: *Epigenetochoerus parvus* (Thorpe), referred, skull and mandible, Y.P.M. 12420 (combination of both sides), from John Day (= approximate age of Harrison), Oregon. $\times\frac{1}{2}$.

FIG. 19. *Merycoidodon* Leidy, *M.* (*Anomerycoidodon*), new subgenus, *M.* (*Blickohyus*), new subgenus, *Paramerycoidodon,* new genus, *P.* (*Barbourochoerus*), new subgenus, *Otionohyus,* new genus, *O.* (*Otarohyus*), new subgenus, *Genetochoerus,* new genus, *G.* (*Osbornohyus*), new subgenus, *Pseudogenetochoerus,* new genus, and *Epigenetochoerus,* new genus. A, *Merycoidodon forsythae,* new species, referred, Wyoming; B, *M. culbertsonii browni,* new subspecies, holotype, Wyoming; C, *M. c. osborni,* new subspecies, holotype, South Dakota; A, *M. culbertsonii* (Leidy), referred, Nebraska, South Dakota, and Wyoming; E, *M.* (*Anomerycoidodon*) *dani,* new species, referred, South Dakota; F, *M.* (*A.*) *lambi,* new species, holotype, South Dakota; G, *M.* (*Blickohyus*) *lynchi,* new species, referred, South Dakota (figs. 20–23 only); H, *Paramerycoidodon georgei,* new species, referred, South Dakota; I, *P.* (*Barbourochoerus*) *major* (Leidy), referred, South Dakota; J, *P.* (*B.*) *wanlessi,* new species, referred South Dakota; K, *Otionohyus wardi,* new species, holotype, Nebraska, referred South Dakota, North Dakota, and Wyoming; L, *O. degrooti,* new species, holotype, Wyoming; M, *?O. vanderpooli,* new species, holotype, Nebraska (figs. 19 and 22 only); N, *O.* (*Otarohyus*) *bullatus* (Leidy), referred, South Dakota; O, *O.* (*O.*) *cedrensis* (Matthew), holotype, Colorado (figs. 20 and 23 only); P, *O.* (*Otarohyus*) *hybridus* (Leidy), referred, South Dakota; Q, *Genetochoerus periculorum* (Cope), referred, Nebraska; R, *G.* (*Osbornohyus*) *norbeckensis,* new species, holotype and referred, South Dakota (figs. 21–23 only); S, *G.* (*O.*) *geygani,* new species, holotype, South Dakota, referred, North Dakota and South Dakota; T, *G.* (*O.*) *dickinsonensis* (Douglass), holotype, Montana (figs. 19, 20, and 22 only); U, *P. covensis,* new species, referred, Oregon; V, *Epigenetochoerus parvus* (Thorpe), referred, Oregon (figs. 19, 20, 22, and 23). (E not illustrated in fig. 19.) $\times\frac{1}{2}$.

FIG. 20. Comparison of skeletal elements (see explanation, fig. 19; J, M, and R not illustrated). $\times\frac{1}{2}$.

FIG. 21. Comparison of skeletal elements (see explanation, fig. 19; J, M, O, S, and T not illustrated). $\times\frac{1}{2}$.

FIG. 22. Comparison of skeletal elements (see explanation, fig. 19; J and O not illustrated). $\times\frac{1}{2}$.

FIG. 23. Comparison of skeletal elements (see explanation, fig. 19; J, M, and T not illustrated). $\times\frac{1}{2}$.

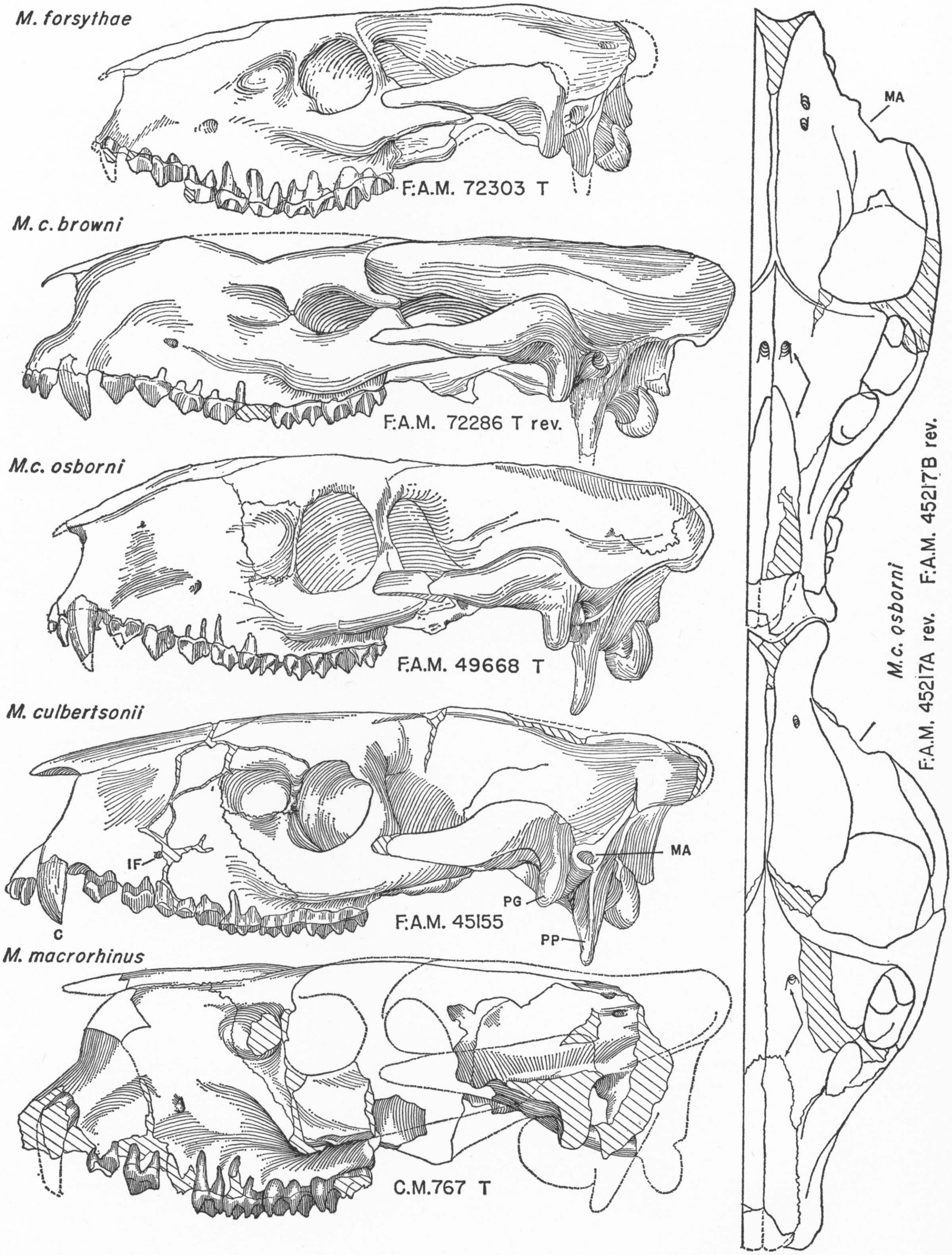

FIG. 1. *Merycoidodon,* three species and two subspecies, holotypes, F:A.M. 72303, 72286, 49668, and C.M. 767, and referred, F:A.M. 45155, 45217A, and 45217B. (See p. 167.) $\times\frac{1}{2}$. (See fig. 2.)

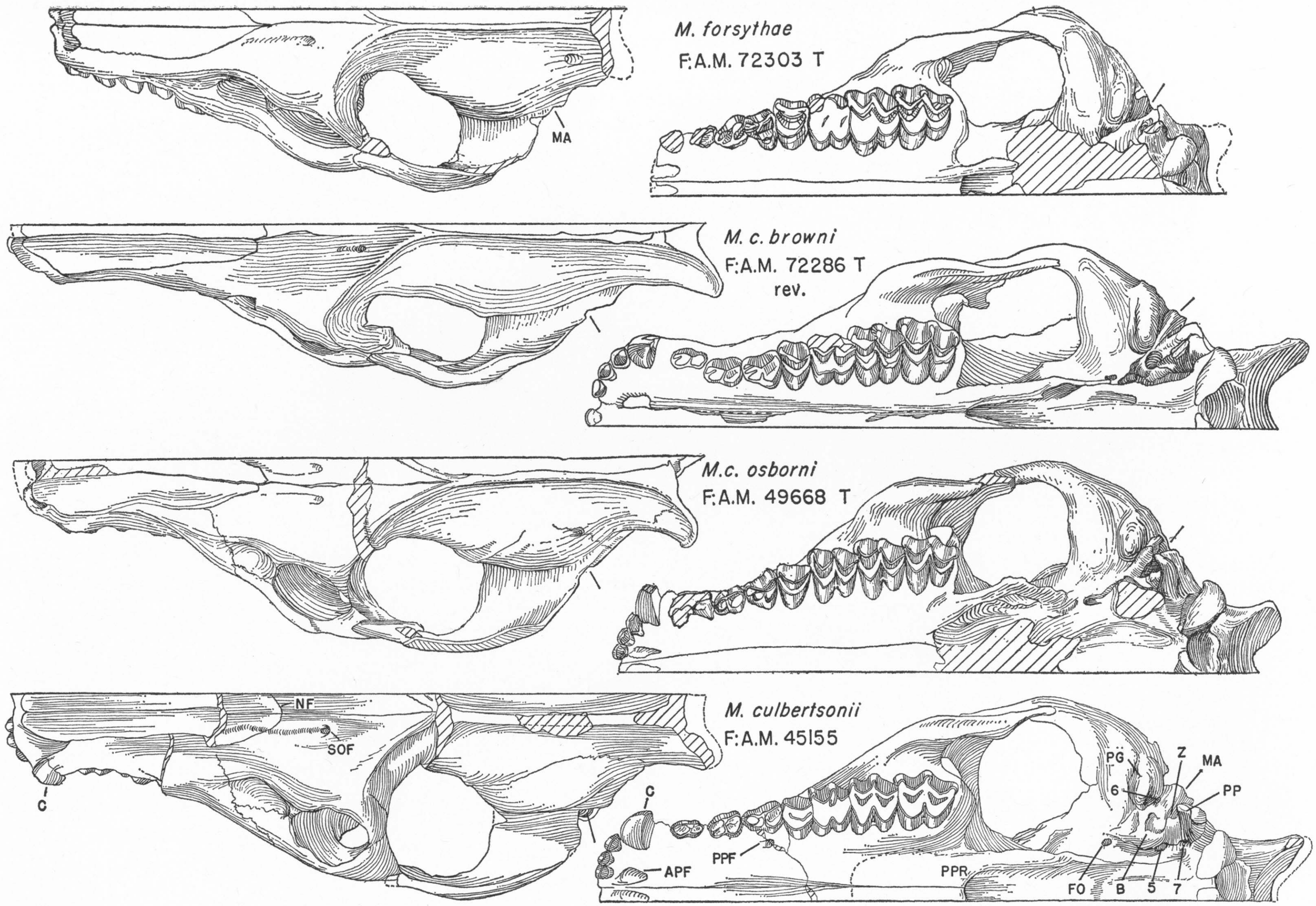

FIG. 2. *Merycoidodon,* two species and two subspecies, holotypes, F:A.M. 72303, 72286, and 49668, and referred, F:A.M. 45155. (See p. 167.) ×½. (See fig. 1.)

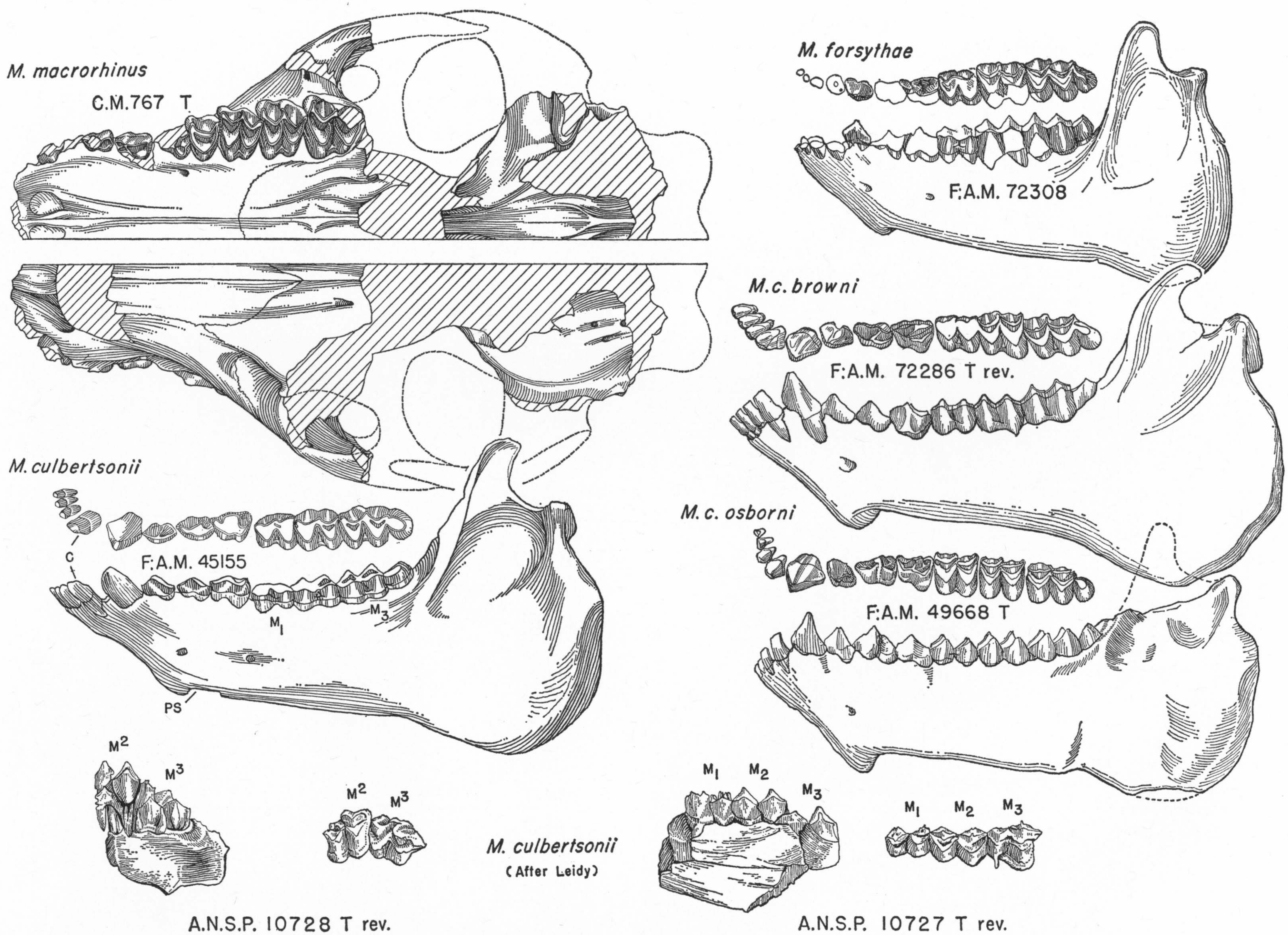

FIG. 3. *Merycoidodon,* three species and two subspecies, holotypes, C.M. 767, A.N.S.P. 10727 and 10728, F:A.M. 72286 and 49668, and referred, F:A.M. 72308 and 45155. (See p. 167.) ×½. (See figs. 1 and 2.)

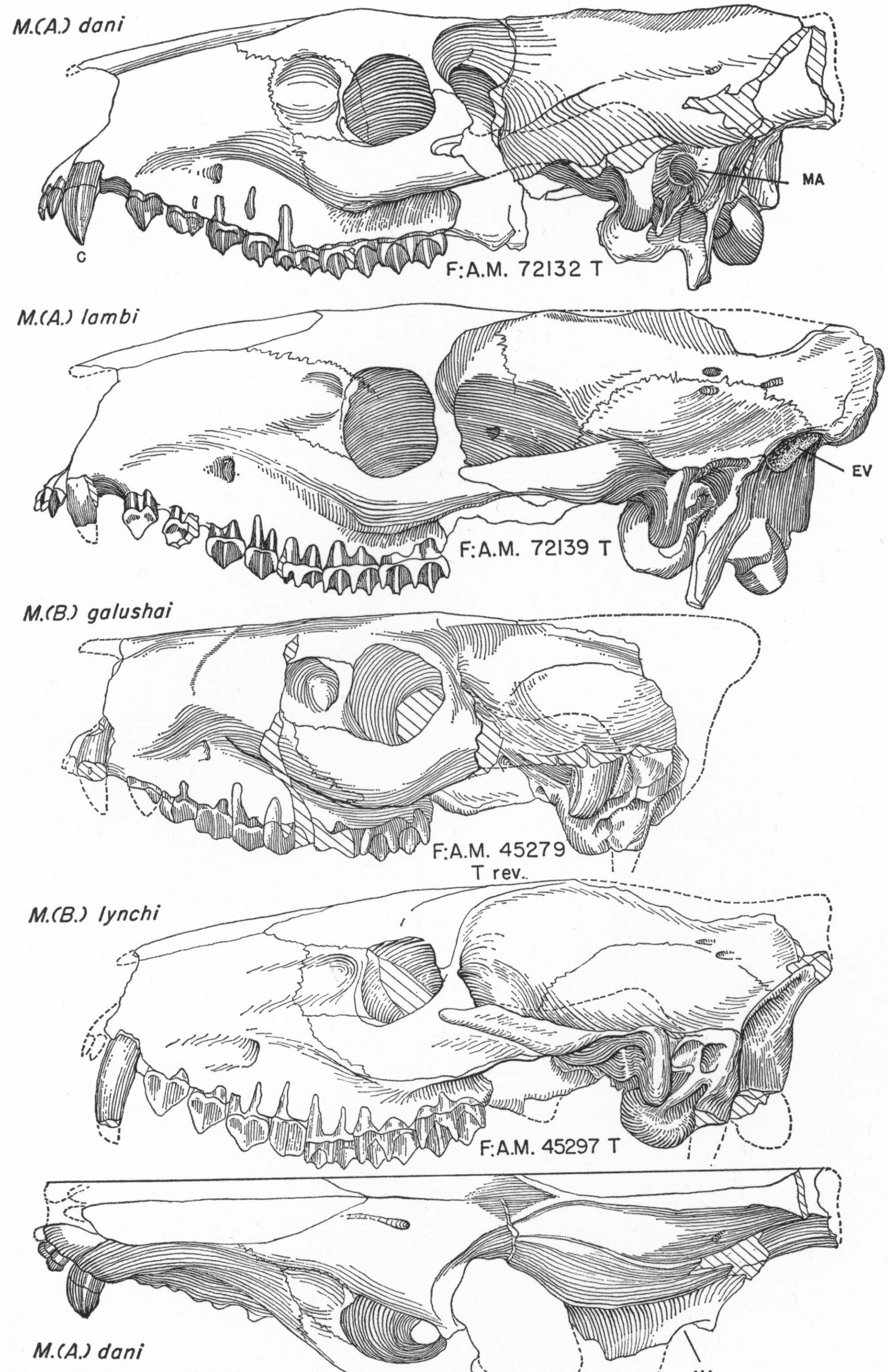

FIG. 4. *Merycoidodon* (*Anomerycoidodon*), two species, holotypes, F:A.M. 72132 and 72139; *M.* (*Blickohyus*), two species, holotypes, F:A.M. 45279 and 45297. (See p. 167.) ×½. (See figs. 5 and 6.)

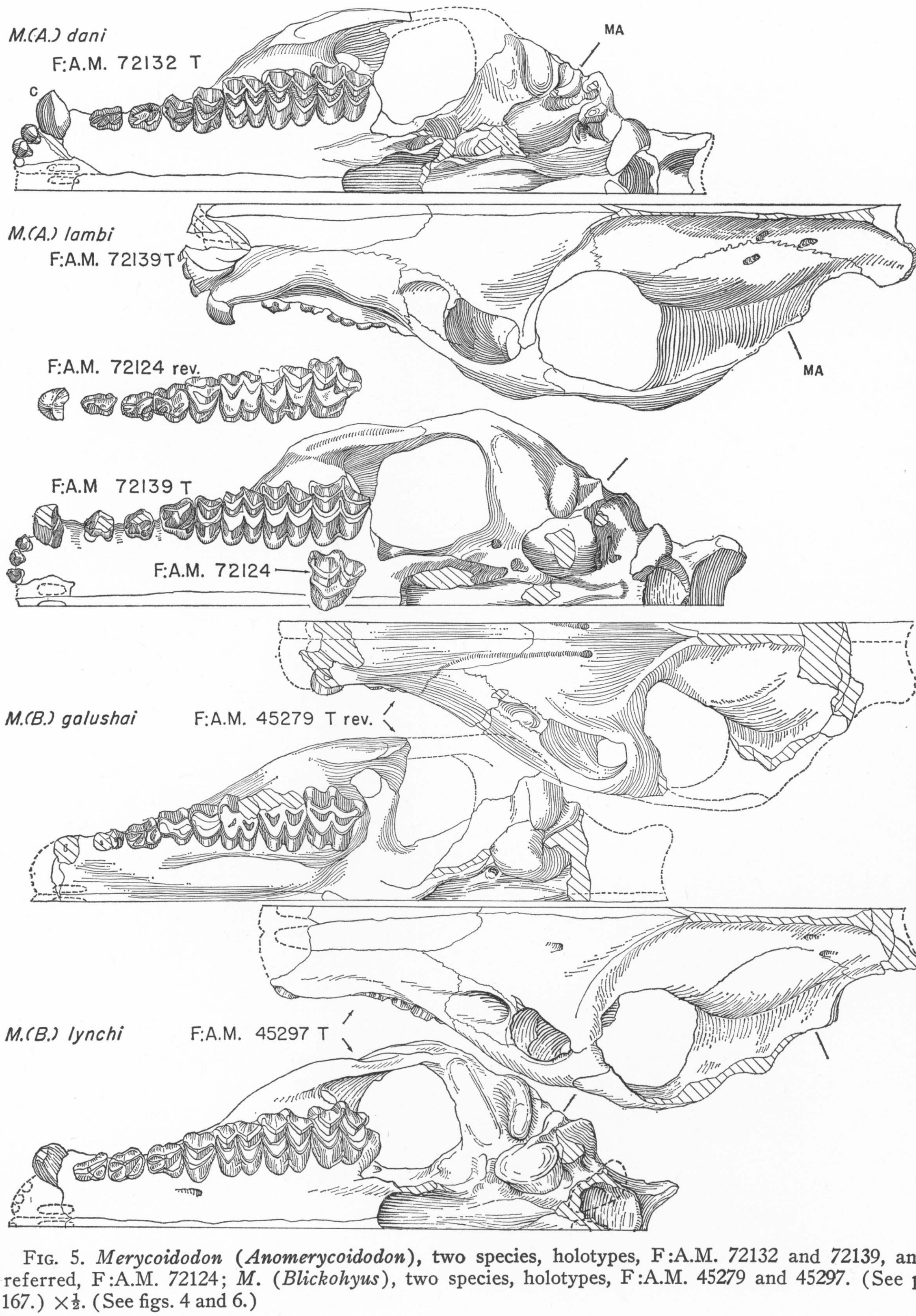

FIG. 5. *Merycoidodon* (*Anomerycoidodon*), two species, holotypes, F:A.M. 72132 and 72139, and referred, F:A.M. 72124; *M.* (*Blickohyus*), two species, holotypes, F:A.M. 45279 and 45297. (See p. 167.) ×½. (See figs. 4 and 6.)

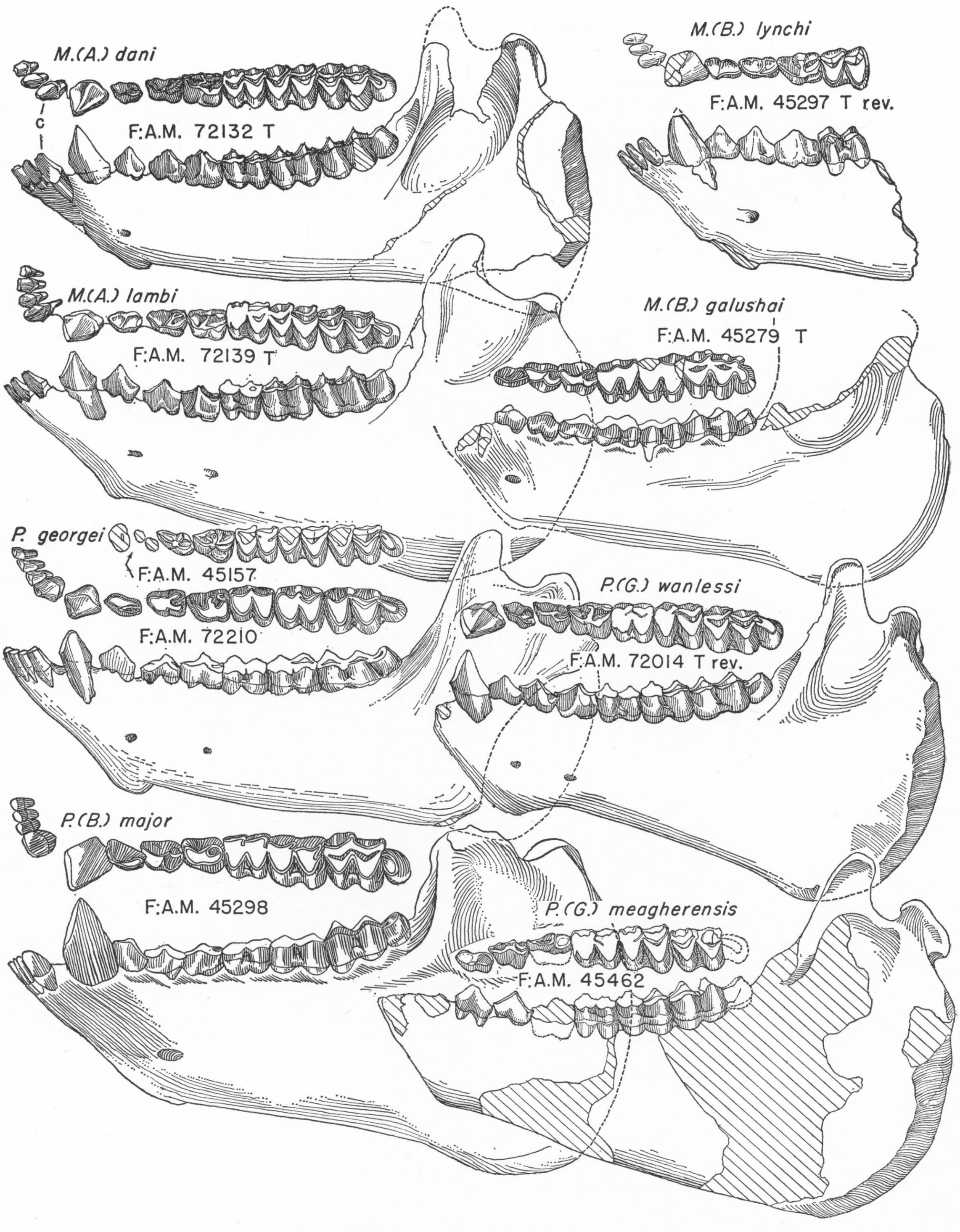

FIG. 6. *Merycoidodon* (*Anomerycoidodon*), two species, holotypes, F:A.M. 72132 and 72139; *M.* (*Blickohyus*), two species, holotypes, F:A.M. 45297 and 45279; *Paramerycoidodon,* one species, referred, F:A.M. 45157 and 72210; *P.* (*Barbourochoerus*), one species, referred, F:A.M. 45298; *P.* (*Gregoryochoerus*), two species, holotype, F:A.M. 72014, and referred, F:A.M. 45462. (See p. 167.) $\times\frac{1}{2}$. (See figs. 4, 5, 7, and 8.)

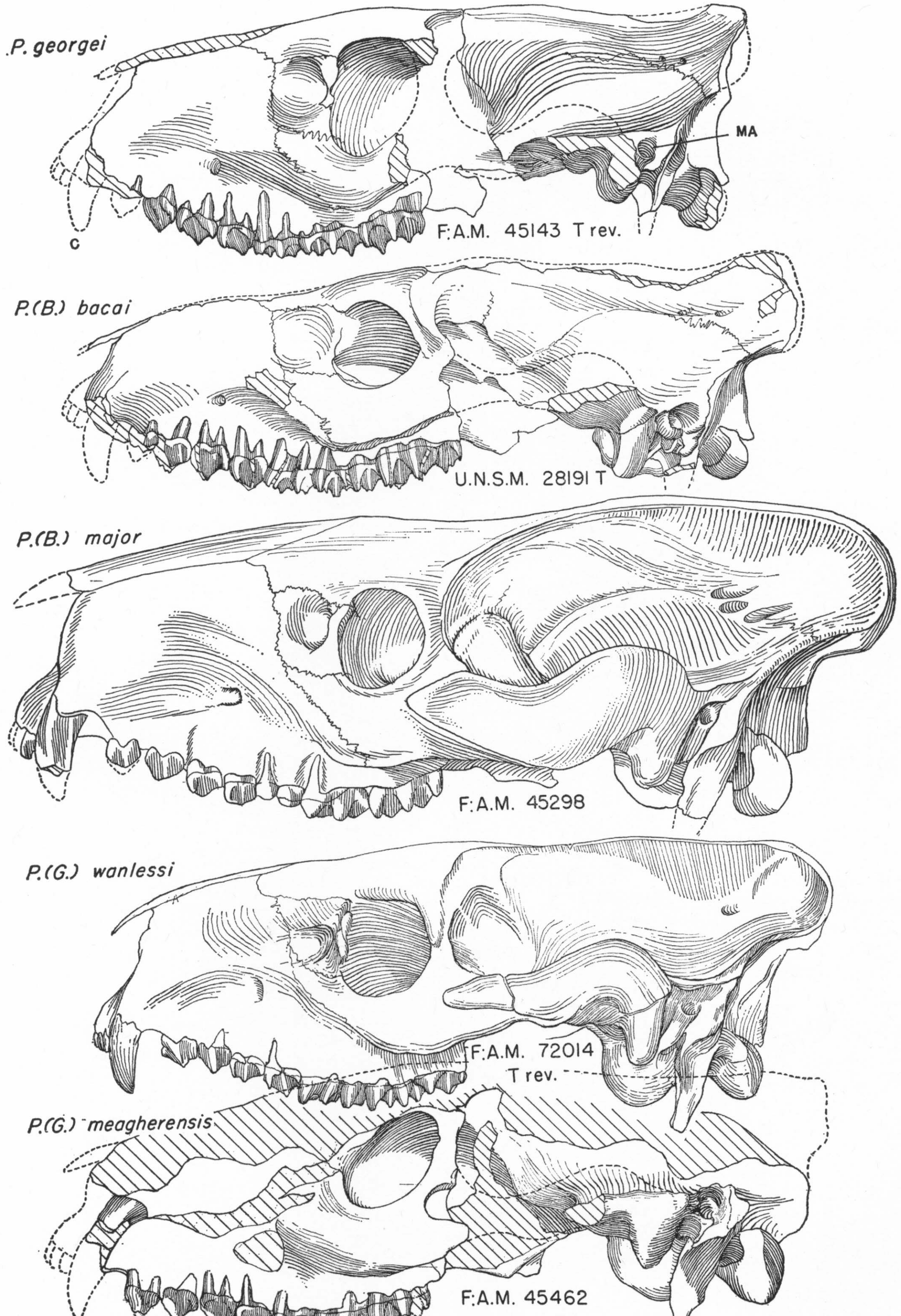

FIG. 7. *Paramerycoidodon,* one species, holotype, F:A.M. 45143; *P.* (*Blickohyus*), two species, holotype, U.N.S.M. 28191, and referred, F:A.M. 45298; *P.* (*Gregoryochoerus*), two species, holotype, F:A.M. 72014, and referred, F:A.M. 45462. (See p. 168.) $\times\frac{1}{2}$. (See figs. 6, 7, and 9.)

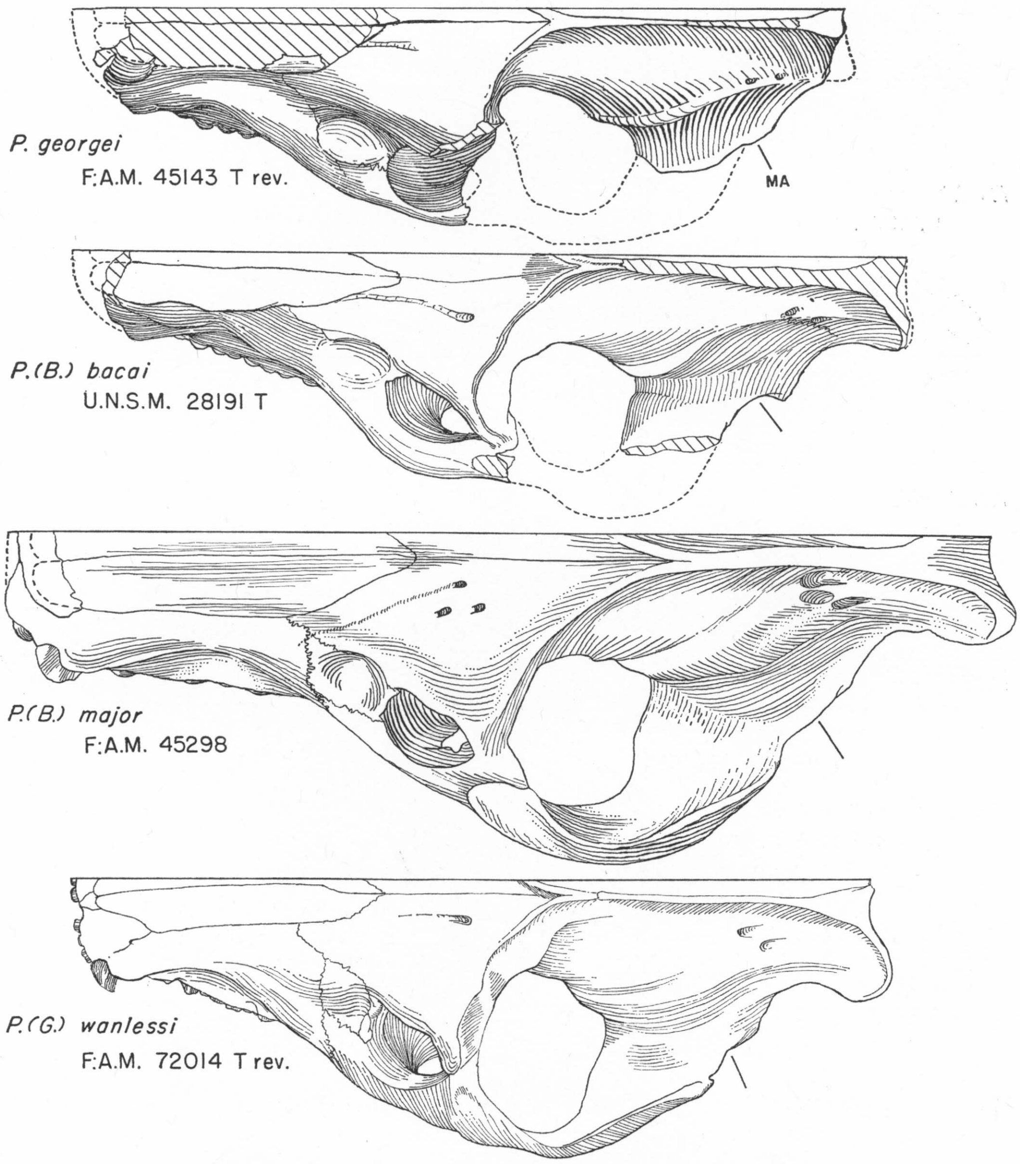

FIG. 8. *Paramerycoidodon,* one species, holotype, F:A.M. 45143; *P.* (*Blickohyus*), two species, holotype, U.N.S.M. 28191, and referred, F:A.M. 45298; *P.* (*Gregoryochoerus*), one species, holotype, F:A.M. 72014. (See p. 168.) $\times \frac{1}{2}$. (See figs. 6, 7, and 9.)

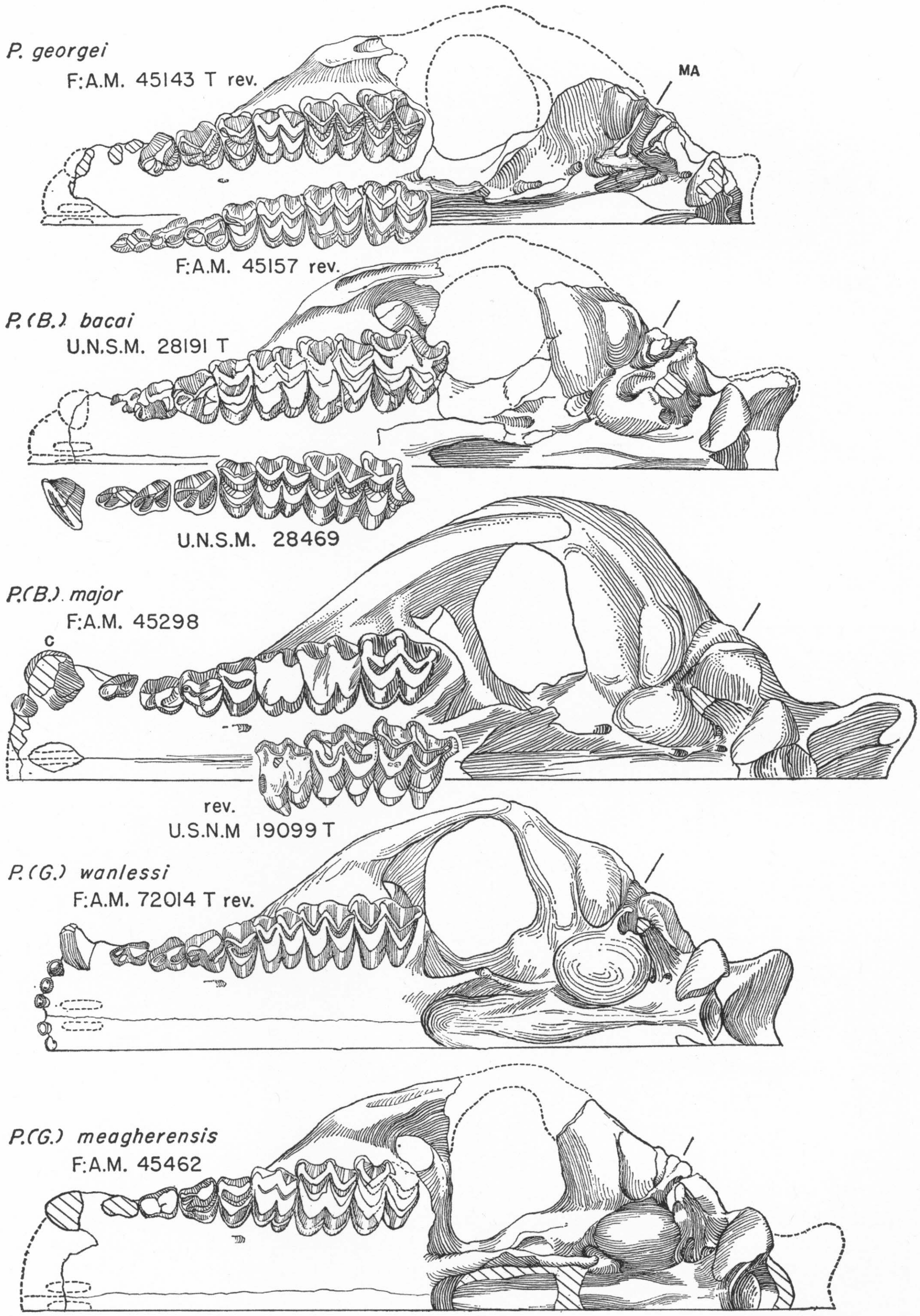

FIG. 9. *Paramerycoidodon,* one species, holotype, F:A.M. 45143, and referred, F:A.M. 45157; *P.* (*Blickohyus*), two species, holotypes, U.N.S.M. 19099 and 28191, and referred, U.N.S.M. 28469 and F:A.M. 45298; *P.* (*Gregoryochoerus*), two species, holotype, F:A.M. 72014, and referred, F:A.M. 45462. (See p. 168.) $\times\frac{1}{2}$. (See figs. 6–8.)

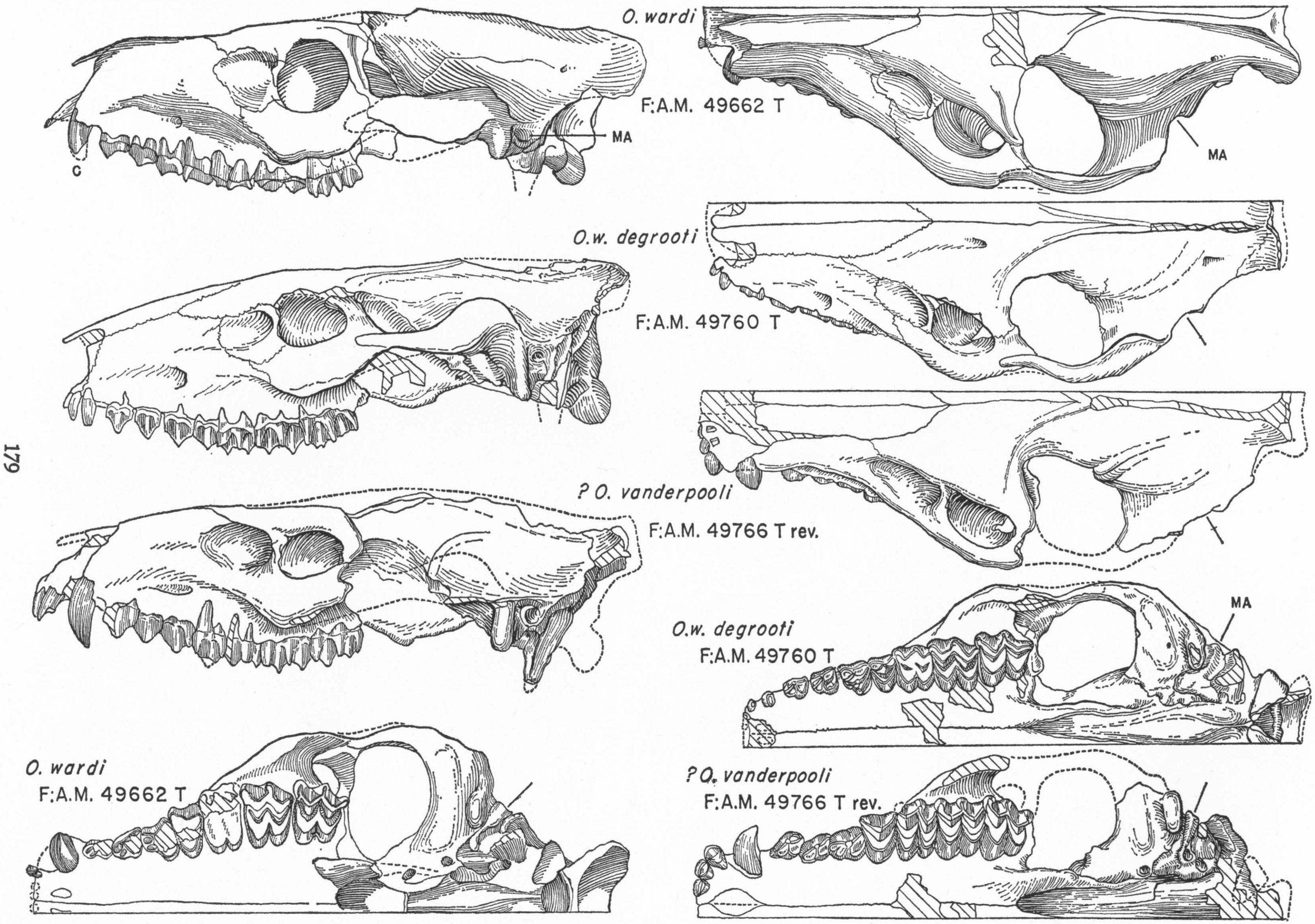

FIG. 10. *Otionohyus,* two species and one subspecies, holotypes, F:A.M. 49662, 49760 and 49766. (See p. 168.) ×½. (See fig. 11.)

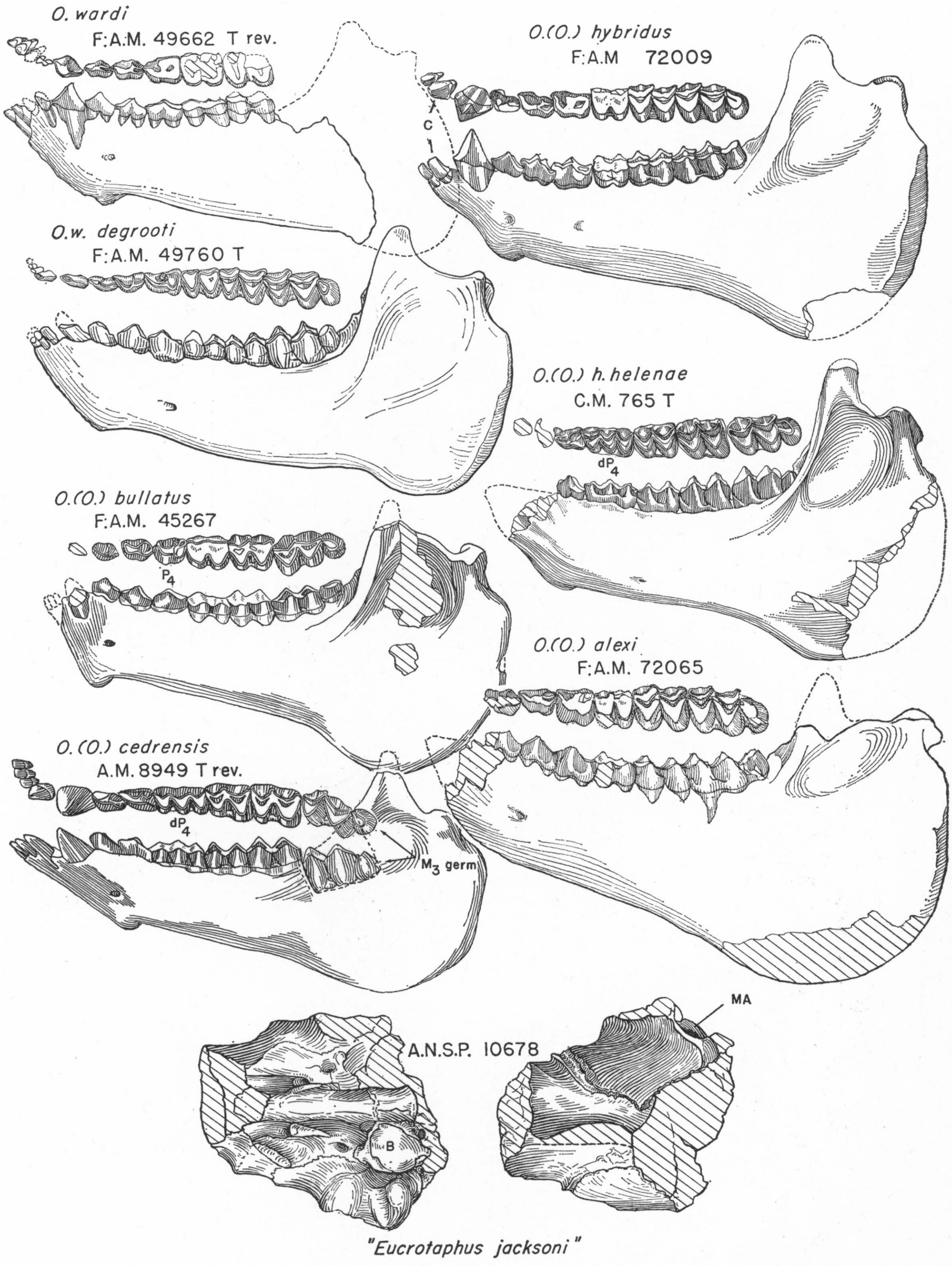

FIG. 11. *Otionohyus,* one species and one subspecies, holotypes, F:A.M. 49662 and 49760; *O.* (*Otarohyus*), four species and one subspecies, holotypes, A.M. 8949 and C.M. 765, and referred, F:A.M. 45267, 72009, and 72065; *"Eucrotaphus,"* holotype, A.N.S.P. 10678. (See p. 168.) ×½. (See figs. 10, 12, and 13.)

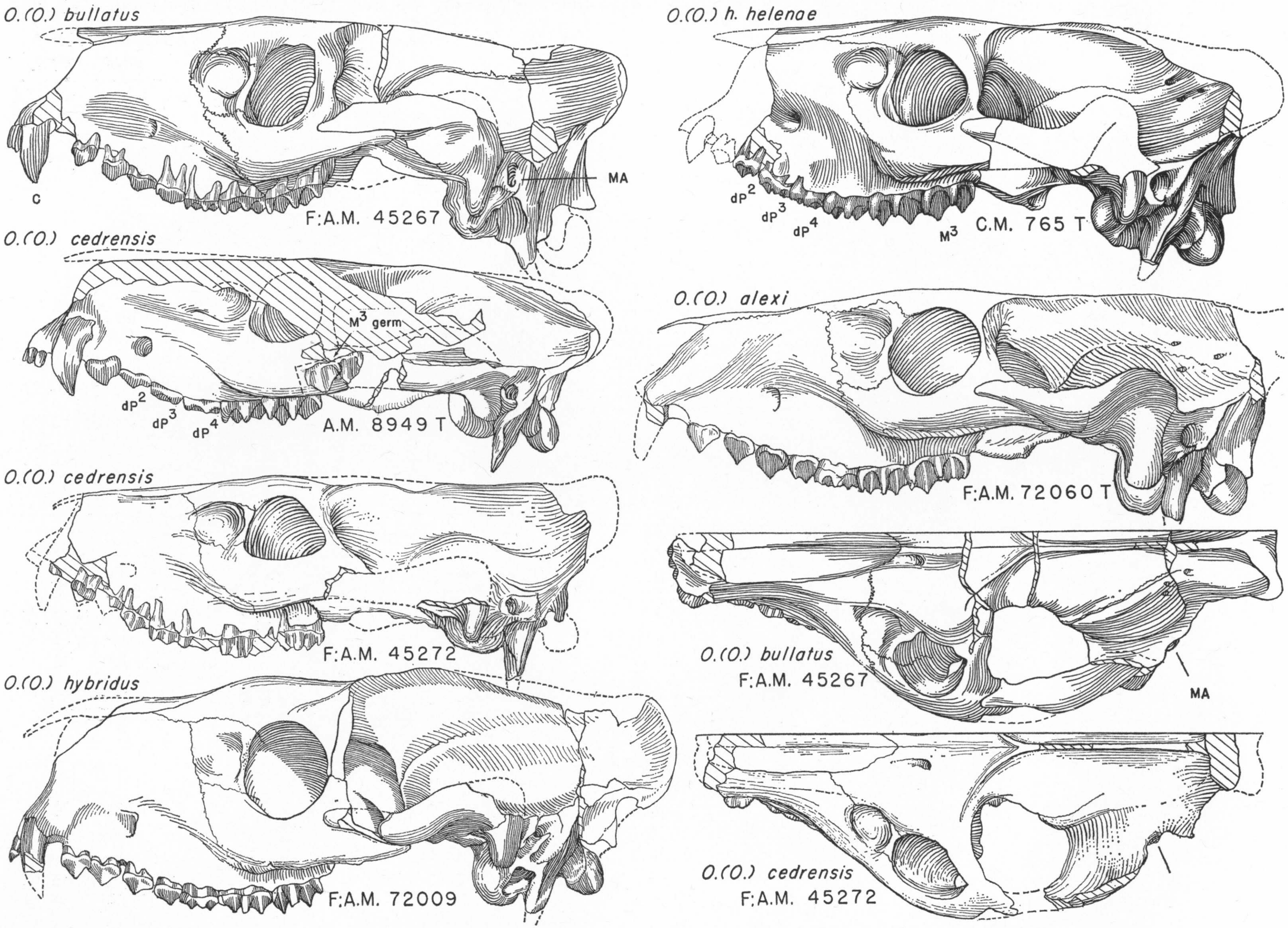

FIG. 12. *Otionohyus* (*Otarohyus*), four species and one subspecies, holotypes, A.M. 8949, C.M. 765, and F:A.M. 72060, and referred, F:A.M. 45267, 45272, and 72009. (See p. 168.) $\times\frac{1}{2}$. (See figs. 11 and 13.)

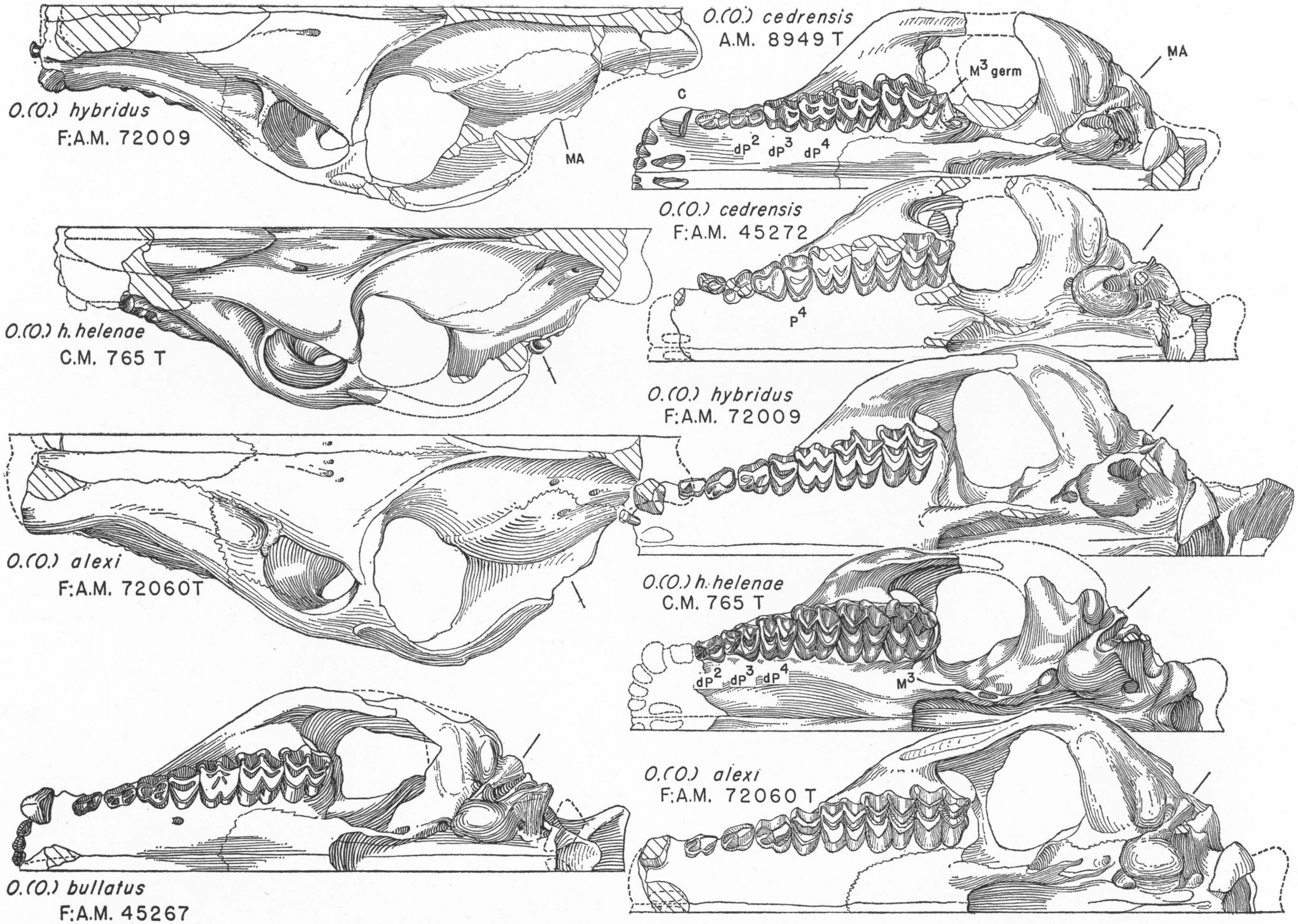

FIG. 13. *Otionohyus* (*Otarohyus*), four species and one subspecies, holotypes, C.M. 765, F:A.M. 72060, and A.M. 8949, and referred, F:A.M. 72009, 45267, and 45272. (See p. 168.) $\times\frac{1}{2}$. (See figs. 11 and 12.)

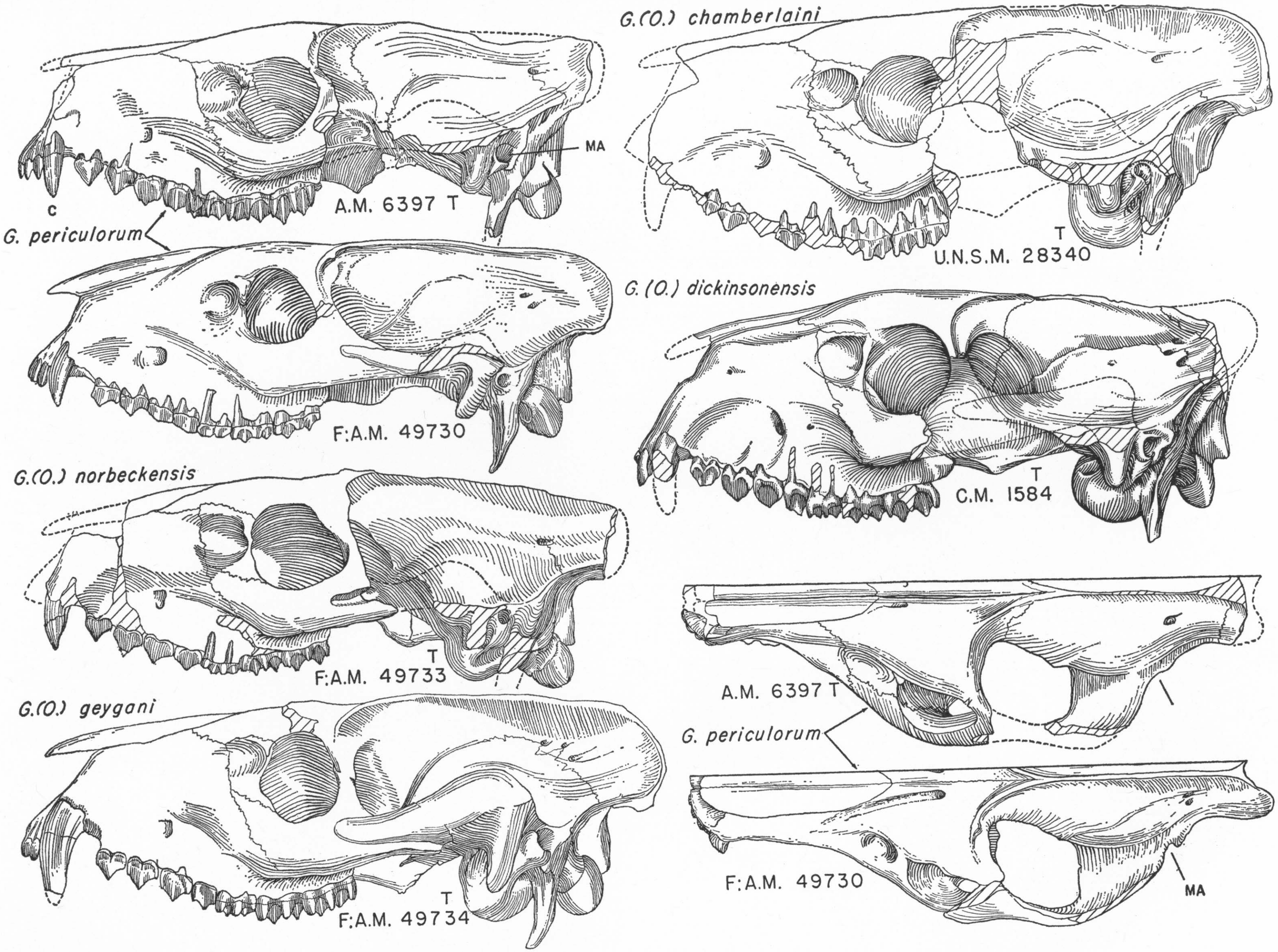

FIG. 14. *Genetochoerus,* one species, and *G.* (*Osbornohyus*), four species, holotypes, A.M. 6397, F:A.M. 49733, 49734, U.N.S.M. 28340, C.M. 1584, and referred, F:A.M. 49730. (See p. 168.) $\times\frac{1}{2}$. (See figs. 14–16.)

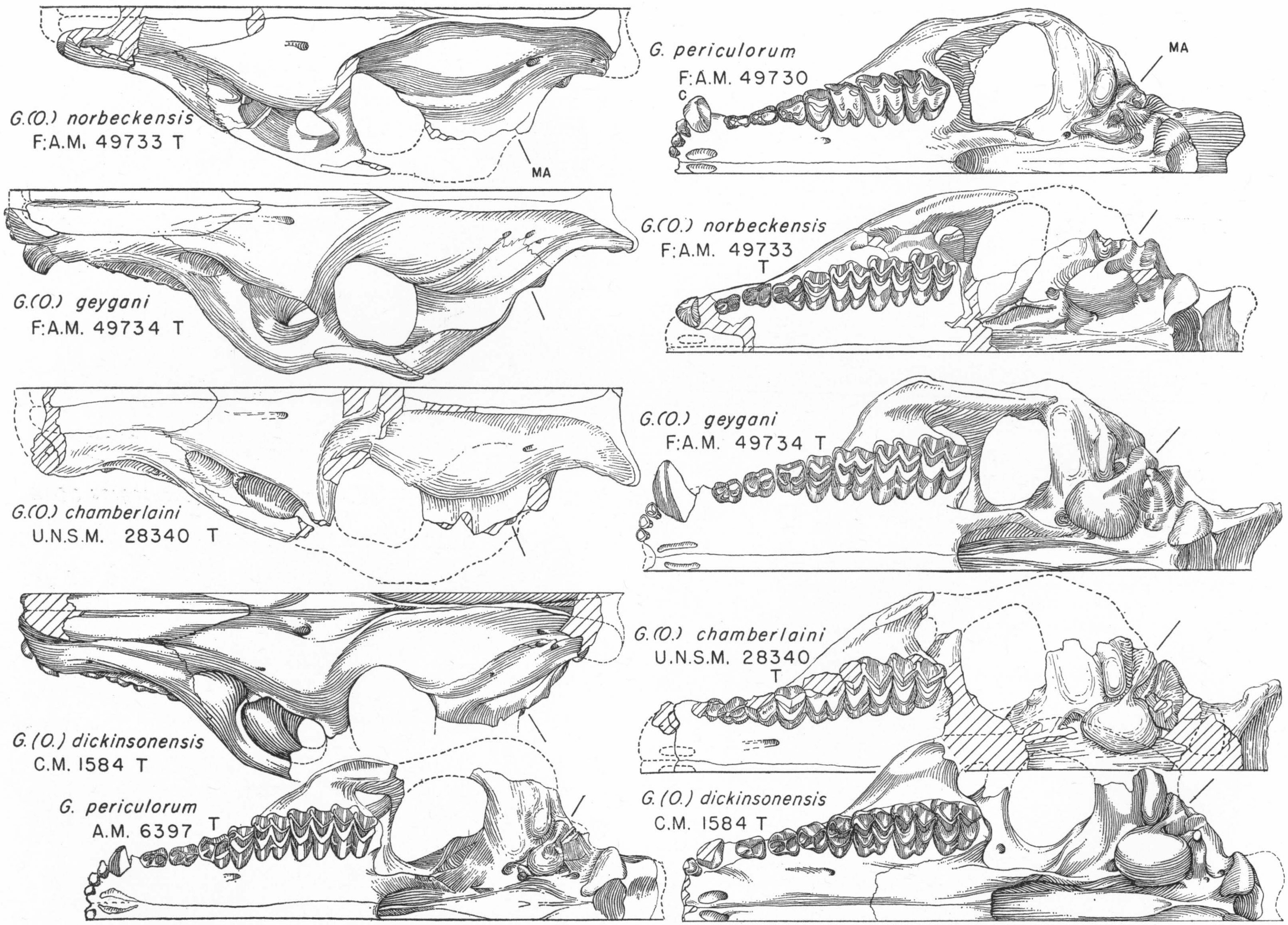

FIG. 15. *Genetochoerus,* one species, and *G.* (*Osbornohyus*), four species, holotypes, F:A.M. 49733, 49734, U.N.S.M. 28340, C.M. 1584, and A.M. 6397, and referred, F:A.M. 49730. (See p. 169.) $\times\frac{1}{2}$. (See figs. 14 and 16.)

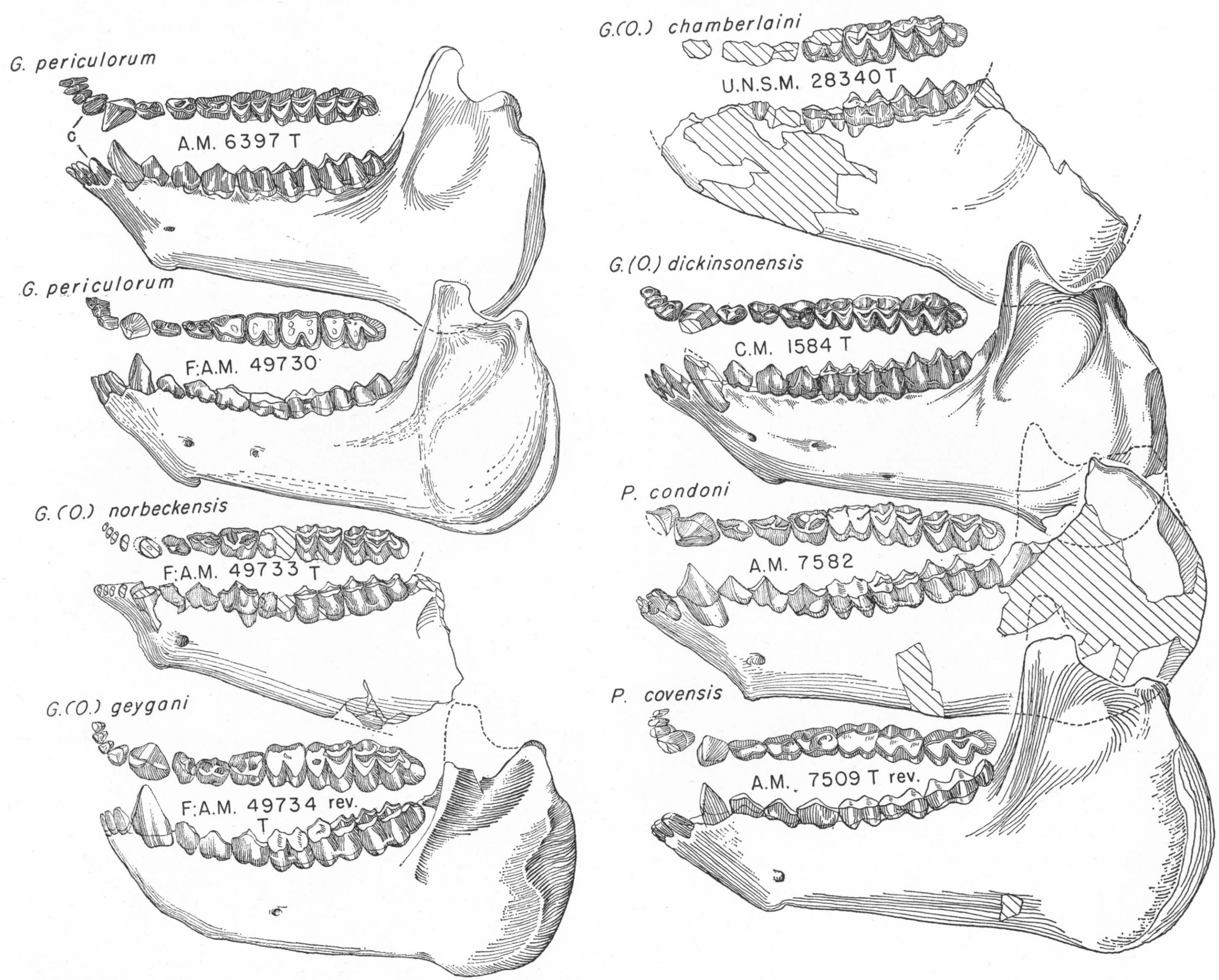

FIG. 16. *Genetochoerus,* one species, *G.* (*Osbornohyus*), four species, *Pseudogenetochoerus,* two species, holotypes, A.M. 6397, F:A.M. 49733, 49734, U.N.S.M. 28340, C.M. 1584, and A.M. 7590, and referred, F:A.M. 49730 and A.M. 7582. (See p. 169.) $\times\frac{1}{2}$. (See figs. 14–15.)

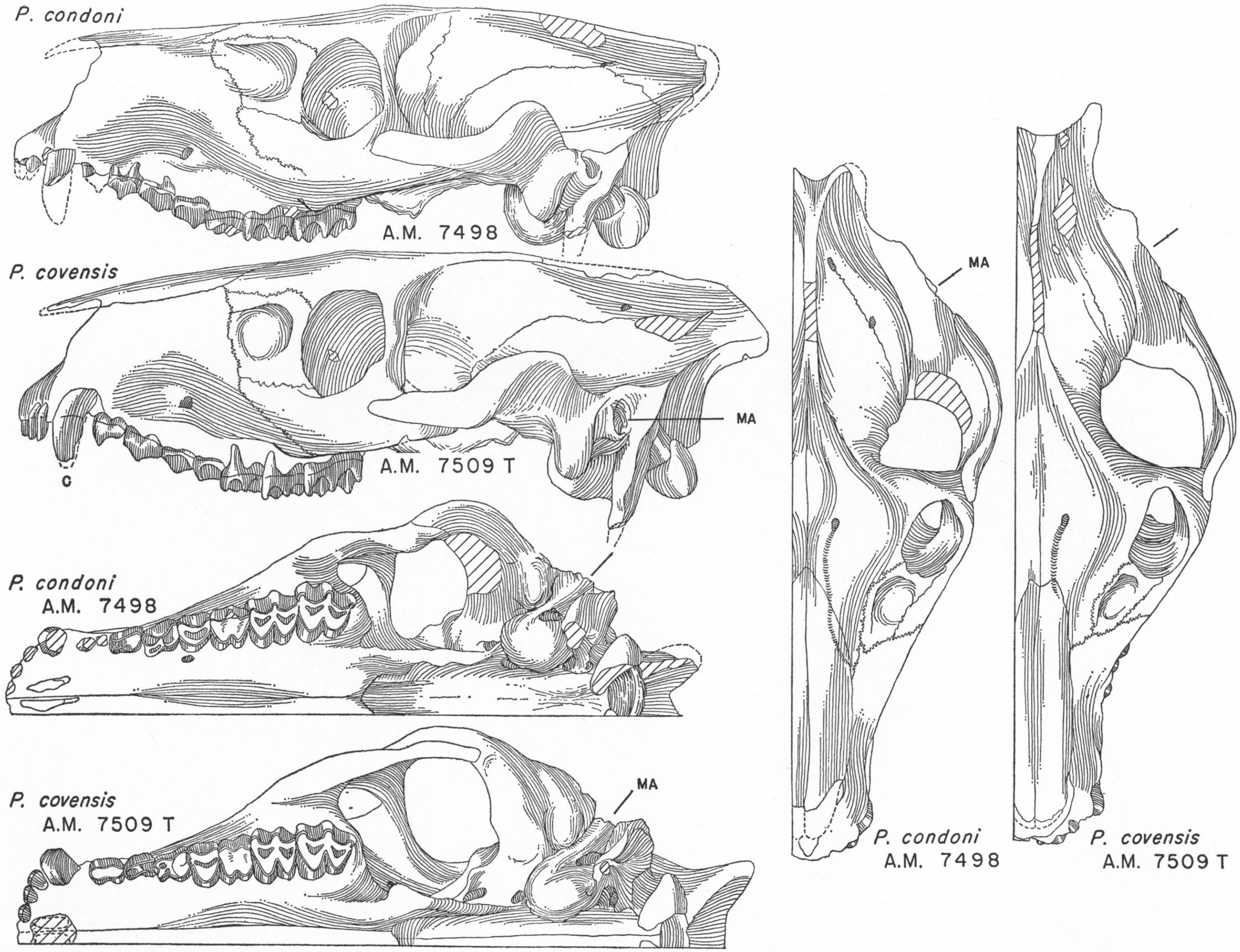

FIG. 17. *Pseudogenetochoerus,* two species, holotype, A.M. 7509, and referred, A.M. 7498. (See p. 169.) ×½. (See fig. 16.)

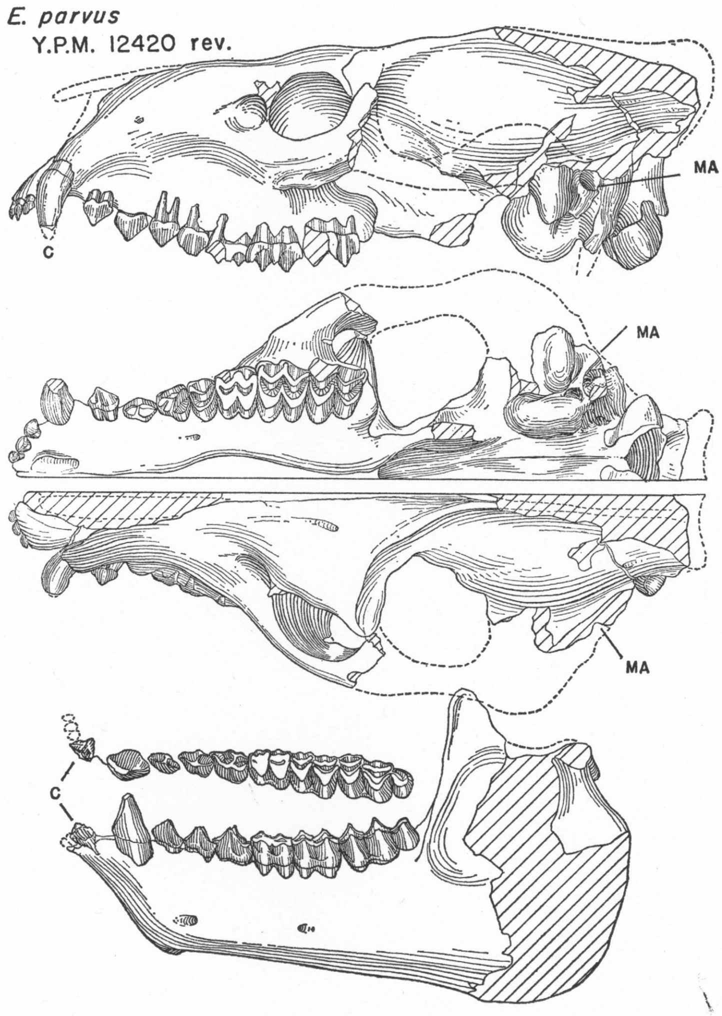

FIG. 18. *Epigenetochoerus,* one species, referred, Y.P.M. 12420. (See p. 169.) ×½.

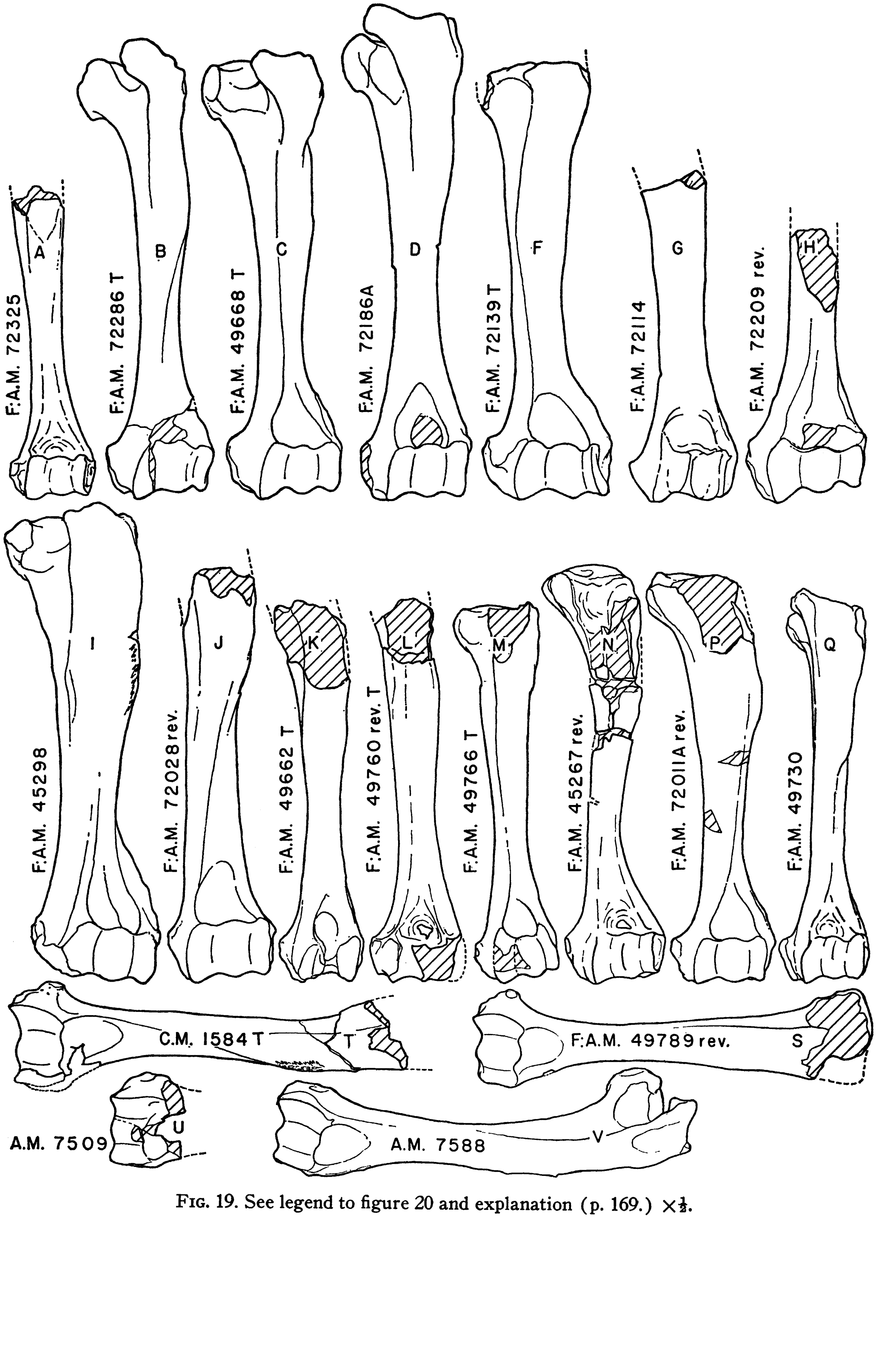

FIG. 19. See legend to figure 20 and explanation (p. 169.) ×½.

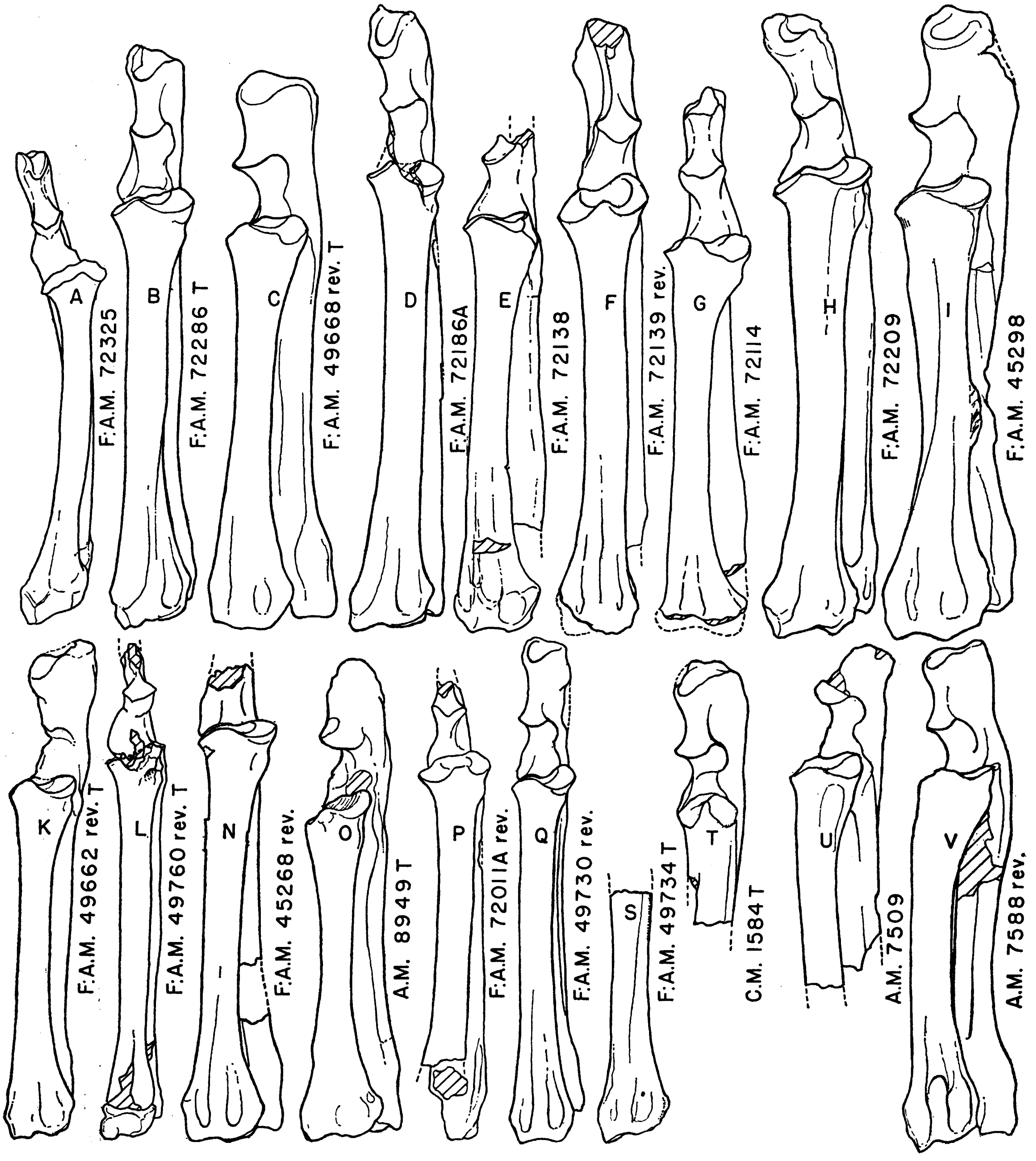

Fig. 20. Comparison of limb elements: A, *Merycoidodon forsythae*; B, *M. culbertsonii browni*; C, *M. c. osborni*; D, *M. culbertsonii*; E, *M.* (*Anomerycoidodon*) *dani*; F, *M.* (*A.*) *lambi*; G, *M.* (*Blickohyus*) *lynchi*; H, *Paramerycoidodon georgei*; I, *P.* (*Barbourochoerus*) *major*; J, *P.* (*B.*) *wanlessi*; K, *Otionohyus wardi*; L, *O. degrooti*; M, *?O. vanderpooli*; N, *O.* (*Otarohyus*) *bullatus*, O, *O.* (*O.*) *cedrensis*; P, *O.* (*O.*) *hybridus*; Q, *Genetochoerus periculorum*; R, *G.* (*Osbornohyus*) *norbeckensis*; S, *G.* (*O.*) *geygani*; T, *G.* (*O.*) *dickinsonensis*; U, *P. covensis*; V, *Epigenetochoerus parvus*. (See p. 169.) $\times\frac{1}{2}$.

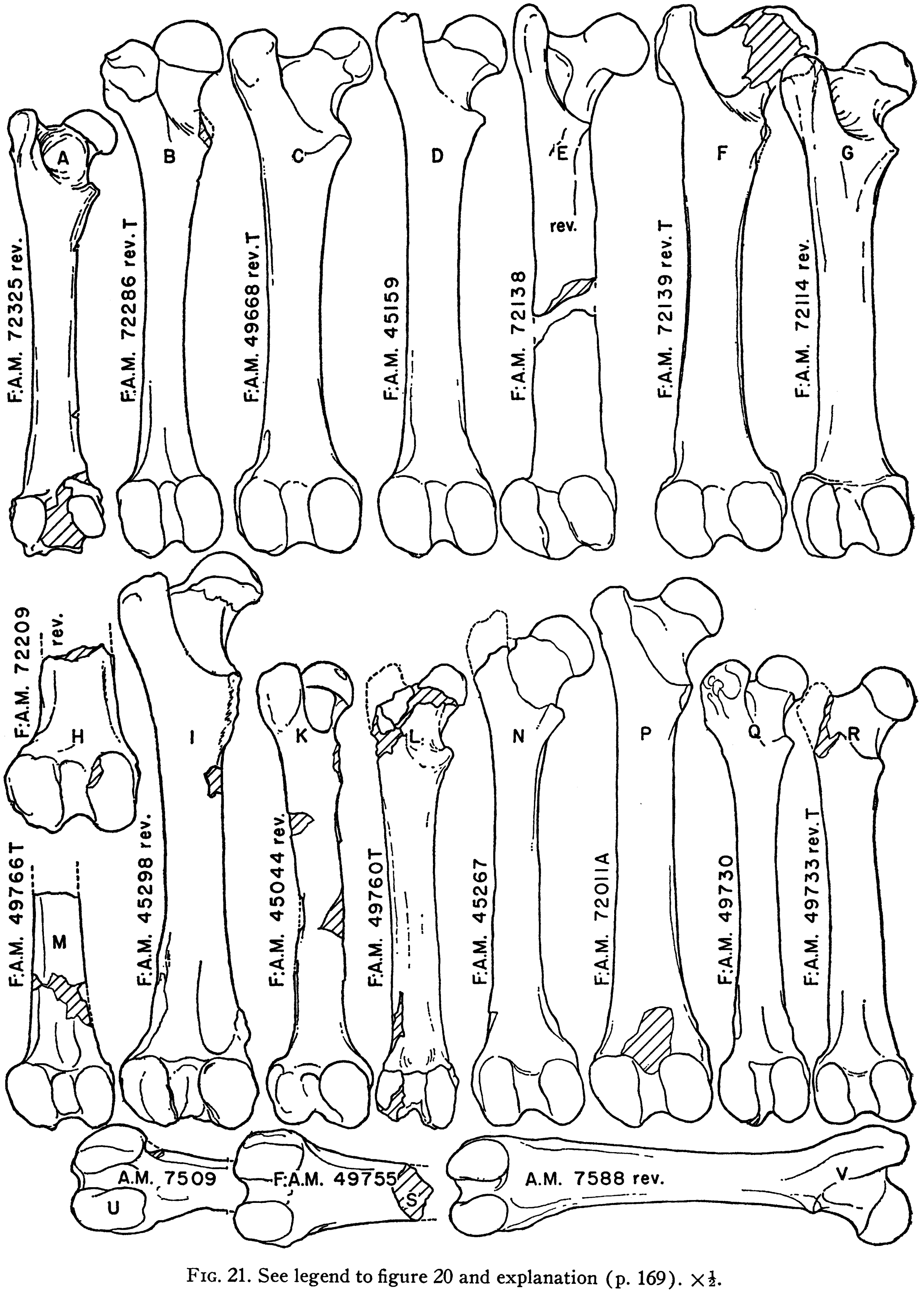

FIG. 21. See legend to figure 20 and explanation (p. 169). $\times\frac{1}{2}$.

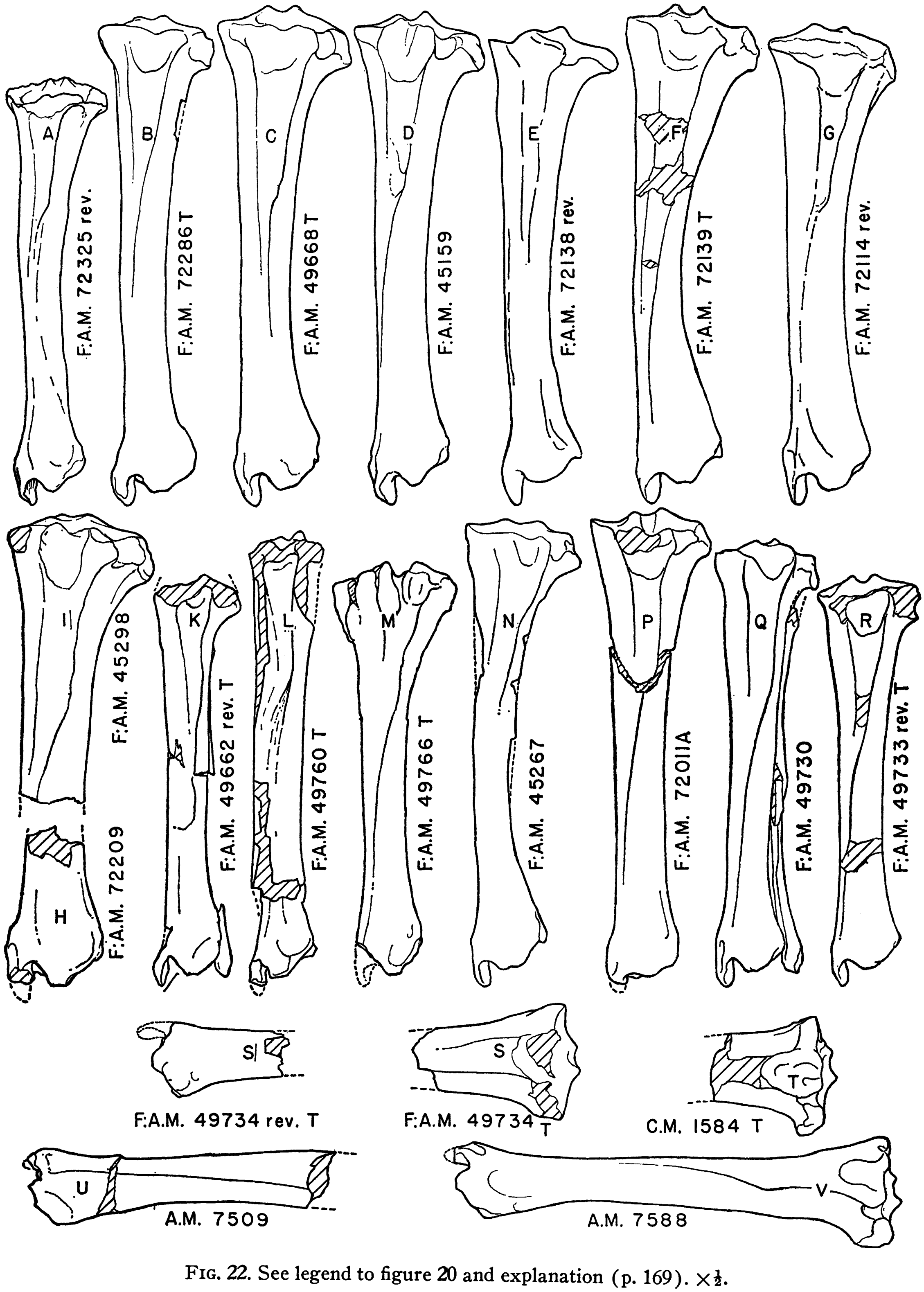

FIG. 22. See legend to figure 20 and explanation (p. 169). ×½.

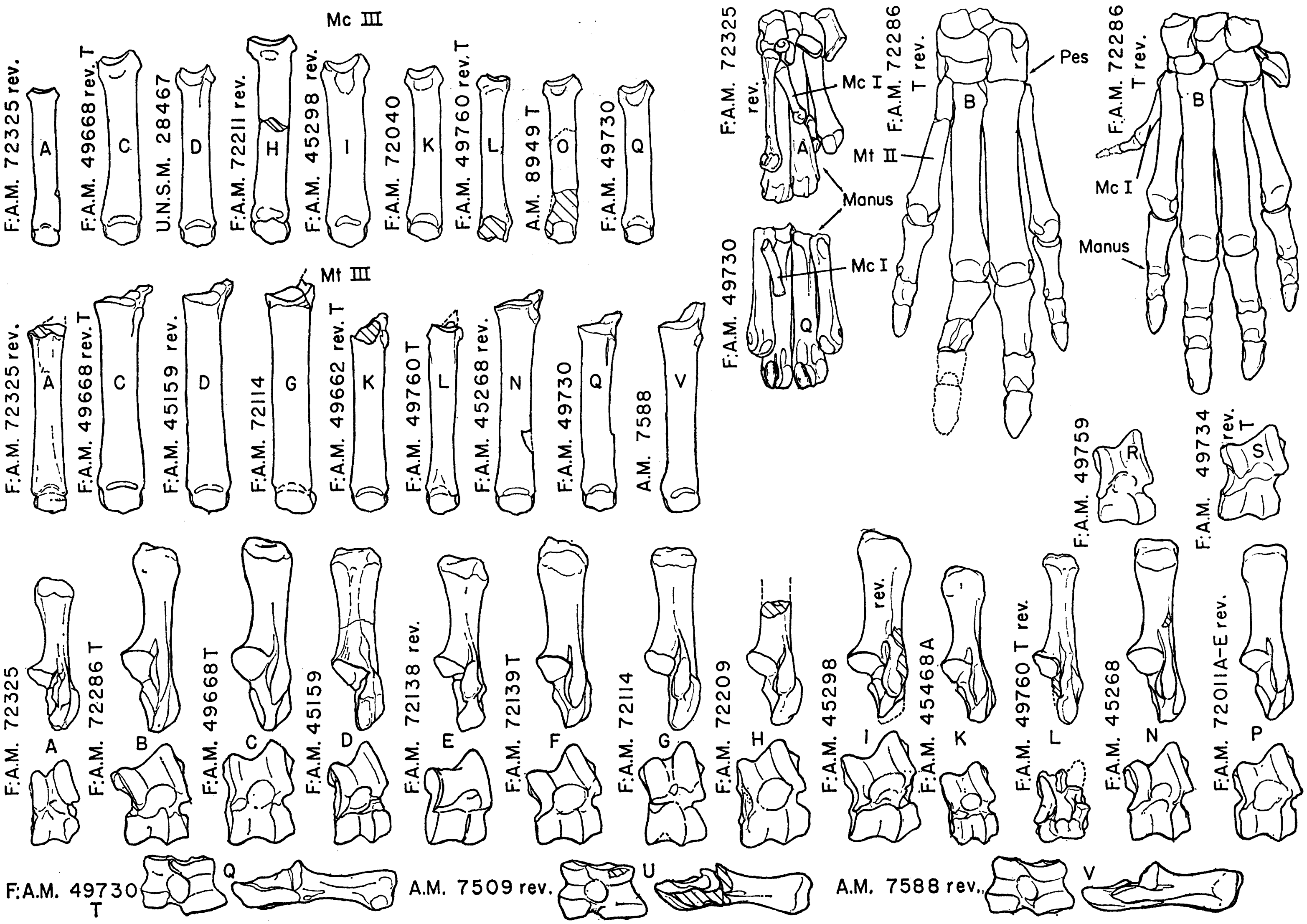

FIG. 23. See legend to figure 20 and explanation (p. 169). $\times\frac{1}{2}$.

DESCRIPTION OF EPOREODONTINAE SCHULTZ AND FALKENBACH, SUBFAMILY 10[1]

THE SUBFAMILY EPOREODONTINAE is restricted to the lower Miocene deposits of the John Day Valley of Oregon, and includes *Eporeodon* Marsh, *E.* (*Paraeporeodon*), new subgenus, and *Dayohyus,* new genus. Skulls of small to medium size; dolichocephalic to brachycephalic; low to medium high; supraoccipital wings with moderate lateral spread, extending from a short to noticeably longer distance posterior to condyle; exoccipital foramen small; brain case well inflated; frontals wide; nasals with slight anterior retraction; anterior nasal-maxilla contact above posterior border of C/ to posterior portion of P^1; supraorbital foramen with anterior groove; orbit roundish, medium to moderately large in size; malar moderately robust below orbit; zygomatic arch from light to moderately robust; infraorbital foramen in area above P^3 to anterior portion of P^4; lacrimal fossa from small to large and from deep to very deep; prominent pit or depression on face above premolar region; muzzle inflated; occipital condyle light; paroccipital process moderately light to heavy (anterior-external surface lacks excavated area found in Merycoidodontinae); bulla well inflated, from semiconical to bulbous in outline; postglenoid process from semi-peg-shaped to compressed anteroposteriorly, external border sloping downward and inward, moderately robust to robust; glenoid surface arched anteroposteriorly; mandible light to robust; postsymphysis below P_3; ramus shallow (deeper than in examples of *Genetochoerus*); apophysis weak, below and posterior to condyle; condyle moderately large, external border slightly higher and slightly more anterior than internal border; dentition brachyodont, light; superior molar, external styles moderately prominent; C/ long (vertically); /C incisiform; P_1 caniniform; molars with deep fossettes; P^1–P^3 each with anterior intermediate crest; M_3 with well-developed heel.

DISCUSSION

The subfamily *Eporeodontinae* is based primarily on *Eporeodon* and *E.* (*Paraeporeodon*) and questionably on *Dayohyus.* All examples of this subfamily are considered to have come from either the middle or upper John Day deposits. In all three phyla evolutionary trends are apparent in specimens from middle to upper John Day. In all instances the horizon is stated questionably as "middle John Day" or "upper John Day."

The three phyla have many characters in common. However, *Eporeodon* and *E.* (*Paraeporeodon*) seem closer to each other than either is to *Dayohyus.* The former two lines have no apparent close affinity (massive skulls with light teeth) to any subfamily present in the Great Plains. *Dayohyus,* however, superficially resembles *Promesoreodon scanloni* from "Zone D" of the Brule. In size, examples of *P. scanloni* are between those of *D. trigonocephalus* and those of *D. wortmani.* If the geologic occurrences were not taken into account, one might well consider *Dayohyus* a new genus within the Promerycochoerinae, contemporary with *Promesoreodon.* The examples of *Promerycochoerus* and *Dayohyus,* however, evidently lived at the same time and may have been derived from the same ancestral stock (*Promesoreodon* from "Zone D" of the Brule).

The geologic occurrence and the possibility of either parallel development or migration of these John Day forms are discussed on page 194 of this report.

It should be noted that the original Cope collection from the John Day is now at the American Museum of Natural History. William D. Matthew's list[2] of the Cope material has been of considerable value in providing the location of collecting areas and also the names of original collectors. The present writers have questioned some of the associations of limb elements and skulls. For example, the same museum number is used for an oreodont skull, a mandible, and limbs, but the limbs can be identified as belonging to a different genus from that of the skull. Perhaps the material was found associated in the field, or it may have become mixed in the subsequent

[1] Schultz and Falkenbach, 1940, p. 215. For references to previously described subfamilies, see pages 19 and 491 of the present report.

[2] "John Day Collection" (Matthew's longhand list), on file in the Osborn Library of the American Museum of Natural History.

DISTINCTIVE CHARACTERS OF THE EPOREODONTINAE[1]

	I. *Eporeodon* (P. 198, figs. 24, 30, 52)	IA. *E.* (*Paraeporeodon*) (P. 204, figs. 25–27, 30, 52)	II. *Dayohyus* (P. 215, figs. 28–30, 52)
Skull, facial region	Moderately low	Slightly higher than in *Eporeodon*	Extremely low to moderately low
Midline protuberance on frontal	Very prominent	Slight or lacking	Lacking
Dentition	Light, brachyodont	Light but slightly more robust than in *Eporeodon*	Light, approximately like that in *Eporeodon*
Limb elements	Comparatively short and light	Longer and more robust than in *Eporeodon*	Approximate length of but lighter than those of *Eporeodon*

handling, cataloguing, and moving of the specimens, which were collected some 90 years ago. Many of the limb associations are, therefore, in doubt. Only the logical associations have been considered valid, and these have been used as the basis of the generic and specific characters of the limbs. When more definite associations of limbs and skulls have been made in the field, the present designation of limb elements can be confirmed or proved incorrect.

The holotype of *Eporeodon* (*Paroreodon*) *leptacanthus* (Cope) was listed by Matthew as a "skull and jaws fine-mouthed," but Thorpe[2] considered that it was a skull without a mandible. Up to the time of the writing of the present report, the mandible had not been found.

Distribution

Remains of the Eporeodontinae so far recognized are restricted to the middle and upper John Day deposits of Oregon. It is here considered that these deposits are approximately equal in age to the Harrison Formation of the Great Plains. The writers[3] have previously stated: "The examples of [*Promerycochoerus*] from the John Day indicate a geologic age approximating that of the Harrison of Nebraska and Wyoming. The forms considered as coming from middle John Day are comparable in size with those from the Harrison, while specimens from the upper John Day are somewhat larger. This may indicate that the upper John Day represents a portion of that interval of time which must be accounted for between the final deposition of the Harrison Formation and the beginning of the Marsland sedimentation in the Great Plains. The upper John Day oreodonts, however, show closer affinities to the Harrison forms than to those of the Marsland."

In the Eporeodontinae, there are no like forms in the Great Plains on which to base conclusions. However, these forms came from the same deposits (John Day) as did the remains of the Promerycochoerinae and the Desmatochoerinae. In all fairness, it must be stated that some of the John Day Eporeodontinae resemble *Genetochoerus* (*Otarohyus*) of the subfamily Merycoidodontinae from the Brule Formation in the Great Plains.

It would seem that the John Day oreodonts evolved independently in the Oregon area, but some forms, such as *Promerycochoerus* and *Desmatochoerus*, may have migrated either into or out of that area. The Eporeodontinae may have evolved locally and remained conservative, thus resembling their Oligocene ancestors. (Many authors have considered the John Day deposits Oligocene in age; see p. 402.)

The absence of the leptauchenins from the John Day also suggests that these Oregon deposits are later than Monroe Creek in age. The leptauchenins are not known from deposits

[1] Compare with Schultz and Falkenbach, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85; 1950, p. 100; 1954, p. 166; 1956, pp. 392, 454; present paper, pp. 25, 234.
[2] 1937, p. 71.
[3] 1949, p. 92, and chart 3.

CHART 7

SIZE RANGE IN THE EPOREODONTINAE.[a] ALL FROM DEPOSITS APPROXIMATELY EQUAL TO THE HARRISON FORMATION, JOHN DAY AREA OF OREGON

	No. of Examples	Skull Basal Length		Dentition P^1–M^3		P_1–M_3		M^3 AP[b]		M_3 AP	
		Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean
I. *Eporeodon*											
E. occidentalis, ?middle John Day	8	172	172	80.5–81	80.5	86	86	18	18	16.5	16.5
E. davisi, ?upper John Day	6	207	207	93	93	88	88	16.5–20.5	18.5	21.5–22	21.5
IA. *E.* (*Paraeporeodon*)											
E. (*P.*) *pacificus*, ?middle John Day	24	187.5–207	203.5	81–97.5	90.5	91–104.5	101.5	19.5–23	20.5	24.5–26.5	25
E. (*P.*) *longifrons*, ?upper John Day	27	208.5–224	217.5	86–119.5	97	102–106.5	104	19.5–23.5	21	22.5–26.5	25
E. (*P.*) *l. perbullatus*, John Day	26	192–209.5	202.5	86.5–96.5	90.5	95–103.5	100	19–21.5	20	20.5–25.5	23.5
E. (*P.*) *leptacanthus*, John Day	18	199.5–215	210.5	90.5–100	96	101–105	103	19.5–21.5	20	23–25	24
II. *Dayohyus*											
D. trigonocephalus, ?middle John Day	9	170–188	178	70–85.5	81	90	90	18–19	18	—	—
D. wortmani, ?upper John Day	10	193–203	197	83.5–89	86	90.5	90.5	16.5–20	18.5	22.5	22.5

[a] All measurements in millimeters.
[b] AP, anteroposterior.

TABLE 8

Eporeodon Marsh, *Eporeodon* (*Paraeporeodon*), New Subgenus, and *Dayohus*, New Genus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*E. occidentalis* Marsh	*E. davisi*, new species	*E.* (*P.*) *pacificus* (Cope)	*E.* (*P.*) *longifrons* (Cope)	*E.* (*P.*) *longifrons perbullatus* (Thorpe)	*E.* (*P.*) *leptacanthus* (Cope)	*D. trigonocephalus* (Cope)		*D. wortmani*, new species
	Holotype Y.P.M. 10142	Holotype A.M. 7576	Holotype A.M. 7502	Holotype A.M. 7504	Holotype Y.P.M. 11011	Holotype A.M. 7695	Holotype A.M. 7505	Referred Y.P.M. 12345	Holotype U.C. 1911
Stage of wear of teeth	(w)	(w‡)	(w‡)	(w+)	(w)	(w)	(w‡‡)	(w)	(w+)
Length (incl. supraoccipital crest and incisors)	((200))[b]	((235))	(245)	252	((239))	250	202	195	(235)
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	((172))[b]	—	202.5	221	(209.5)	206	175	170	203
Width (max.)	((118))	((150))	138	((132))	((125))	((118))	146	(136)	154
Width of brain case (max.)	57	65	63	65	65	58	62	59.5	66.5
Width (interorbital) min.	61.5	72.5	65.5	67	((68))	(54)	54.5	58.5	62.5
Distance from anterior rim of orbit to anterior base of C/	((75))[b]	((83))	86.5	98.5	95.5	88	73	69	87
Distance from anterior rim of orbit to supraoccipital crest	((125))	((153))	(155)	(160)	—	151	127	121	(150)
Length of nasals	(64)	(82)	93	93.5	?	86.5	(67)	—	85
Width of muzzle at infraorbital foramina	59.5	62	55	58	64.5	(51)	52	55	58
Width across canines	—	—	(52)	—	(45)	42.5	((46))	(52)	52
Length, C/–M^3 incl.	((92))	((94))	106.5	112.5	109	110.5	((84))	94	104.5
Length, P^1–M^3 incl.	((81))[b]	((88))	90.5	94	91	95.5	((70))	80.5	(87.5)
Length, P^1–P^4 incl.	((39))[b]	(42.5)	45	47.5	44.5	46	40	39.5	(42.5)
Length, M^1–M^3 incl.	42	(43.5)	47.5	47.5	48	51	32	45	45
Width of M^3 (max.)	16.5	16.5	19	18.5	18	19	—	—	17.5
Depth of malar below orbit	18	18.5	17.5	17	15	15.5	15	15.5	16

TABLE 8—(*Continued*)

MANDIBULAR RAMUS	*E. occidentalis* Marsh	*E. davisi*, new species	*E. (P.) pacificus* (Cope)	*E. (P.) longifrons* (Cope)	*E. (P.) longifrons perbullatus* (Thorpe)	*E. (P.) leptacanthus* (Cope)	*D. trigonocephalus* (Cope)		*D. wortmani*, new species
	Referred Y.P.M. 11024	Referred A.M. 7689	Referred A.M. 7783	Referred A.M. 7591	Holotype Y.P.M. 11011	Referred A.M. 7694	Holotype A.M. 7505	Referred Y.P.M. 12345	Referred A.M. 7655
Stage of wear of teeth	(w)	(−M)	(w+)	(w‡+)	—	(w‡)	—	—	(w+)
Length (max., incl. incisors)	151	(172)	186	194.5	—	187	—	162	((170))
Length, /C–condyle incl.	139	149	171.5	175.5	—	—	—	147.7	(151)
Depth of jaw under coronoid	—	87.5	(80)	86.5	—	—	—	—	(81.5)
Depth of jaw below anterior edge of M_3	32	33.5	32.5	34.5	32.5	36.5	—	38	33.5
Length, /C–M_3 incl.	93.5	98.5	115.5	113	—	((108))	—	99	(95)
Length, P_1–M_3 incl.	86	93	104	103.5	103	103.5	—	90	90.5
Length, P_1–P_4 incl.	40	45.5	50	49.5	49.5	47.5	—	41.5	42
Length, M_1–M_3 incl.	47	51	55	53	54	56	—	49	48

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] Estimates based on Y.P.M. 11024.

TABLE 9

Eporeodon MARSH, *Eporeodon* (*Paraeporeodon*), NEW SUBGENUS, AND *Dayohyus*, NEW GENUS. COMPARATIVE MEASUREMENTS[a] OF SKELETAL ELEMENTS

	E. occidentalis Marsh Referred A.M. 7661	*E. davisi*, new species Referred A.M. 7641	*E.* (*P.*) *pacificus* (Cope) Referred A.M. 7783	*E.* (*P.*) *longifrons* (Cope) Referred A.M. 7591	*E.* (*P.*) *leptacanthus* (Cope) Referred A.M. 7636	*D. wortmani*, new species Referred A.M. 7655
Length of humerus (articular)	134.5	—	148.5	—	150	144.5
Length of radius (articular)	—	—	—	—	134	—
Length of ulna (max.)	—	—	—	—	177	—
Length of metacarpal III (max.)	—	—	69.5	—	—	—
Length of femur (articular)	—	—	187	(181.5)	((182.5))	—
Length of tibia (articular)	—	143.5	172.5	—	—	—
Length of metatarsal III (max.)	—	—	79	—	—	—
Length of calcaneum (max.)	48.5	—	((60))	62	63.5	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

equal in age to the Harrison in either the Great Plains or the West Coast areas. Leptauchenins are recorded from the lower Miocene (Sespe) sediments of California. (For a discussion of the stratigraphic relationships of the Leptaucheniiae, see chart 8, and p. 235).

I. EPOREODON MARSH

Eporeodon MARSH, 1875, p. 249. THORPE, 1937, p. 62.

Paracotylops MERRIAM, 1901b, p. 297.

GENOTYPE: *Eporeodon occidentalis* Marsh.

CHARACTERS

SKULL: Small to medium in size; basal lengths ranging from 171 to 207 mm., widths from 125 to 160 mm.; mesocephalic; facial region medium high; supraoccipital wings extending posteriorly for short distance posterior to condyles, wings small and slightly spread [more noticeably so than in examples of *E.* (*Paraeporeodon*) and *Dayohyus*]; sagittal crest moderately high and heavy; superior contour of skull arched, with highest point above orbits; frontal broad, with noticeable protuberance at midline above posterior border of orbit (similar to the Miocene forms of the Desmatochoerinae; protuberance absent from the Oligocene forms of the Desmatochoerinae); nasals wide, posterior border obtuse; orbit roundish, directed mostly outward; infraorbital foramen above anterior portion of P^3 to mid-portion of P^4; lacrimal fossa moderately large and exceptionally deep; muzzle extremely inflated; paroccipital process moderately wide at base, tapering downward to a sub-round shaft; bulla inflated, semi-conical in shape; postglenoid massive, peg-shaped to laterally expanded; palate extending posteriorly from posterior border of M^3 to well behind that point.

MANDIBLE: Moderately light (especially in comparison with the more massive skull); postsymphsis below P_3; inferior border of ramus increasing in depth posteriorly, with abrupt downward curve posterior to M_3; condyle moderately light, long transversely.

DENTITION: Brachyodont; light, noticeably so for size of skull; I_1–P_1 spatulate; external styles of superior molars light but prominent.

LIMBS[1]: Moderately short (approximately equal to those referred to *Epigenetochoerus parvus*, p. 164); moderately light.

MEASUREMENTS: Tables 8, 9 (pp. 196 and 198).

[1] It should be noted that the association of limb elements with dentitions could well be questioned. It is evident that some small skulls of *Epigenetochoerus* have been found associated with limbs that undoubtedly belong to large examples of *Promerycochoerus*.

ILLUSTRATIONS: Figures 24, 52 (skulls, mandibles, and dentitions), 30 (limbs).

DISCUSSION

The genus *Eporeodon* has been a "catch-all" for various types of Oligocene and lower Miocene oreodonts. The present writers believe, however, that oreodont remains referable to this genus and to *Dayohyus* are restricted to the middle and upper John Day (lower Miocene) deposits of the Oregon region.

Originally, the John Day deposits were considered as Oligocene in age. Matthew,[1] however, suggested that the faunas of the upper and middle John Day were "very largely identical with [the fauna] of the lower Rosebud." Thorpe[2] thought the middle John Day deposits might be upper Oligocene, and that it was possible to determine the geologic horizon of specimens in the various collections by the color of the adhering matrix. The green matrix was considered to be from the middle John Day and the light gray from the upper. The present writers,[3] however, have examined specimens with both green and gray matrix adhering to the fossils, so it is apparent that color of matrix is not a valid criterion for placing the forms geologically. Morton Green[4] came to the same conclusion concerning John Day fossils and stated, "Matrix colors on mammal specimens have been used as stratigraphic indicators, which is now untenable." It appears that the John Day deposits are badly faulted and that a green layer on one hill may or may not be the same green layer on the next, and that a green layer in one locality may even be correlated with a gray layer in another. Unfortunately most of the available specimens from the John Day had little or no geological information associated with them.

In view of the foregoing problems due to the lack of adequate geologic data associated with the John Day oreodonts, the writers consider their identification of the referred specimens to the various species as tentative. It is extremely difficult to identify a particular skull based on measurements only, without information concerning its geologic occurrence. If geologic data are not available, the research worker is not certain whether he is dealing with individual variation of forms that lived at essentially one time, geologically speaking, or with variation due to differences in stratigraphic levels.

[1] 1924, p. 751.
[2] 1937, pp. 66, 70–72, 81, 83, 84, 91.
[3] 1949, pp. 88, 93.
[4] 1950.

Although the present writers are naming two new species, they do believe that too many forms have been named within the Eporeodontinae. Some species may be in synonymy, or perhaps another phylum is involved. In the specimens here tentatively referred, there is considerable variation in the dentitions, the auditory bullae, and other morphologic characters. Hence, all examples here listed under a species or subspecies are tentatively referred.

The following list is the stratigraphic occurrence of the John Day oreodonts as interpreted by the present writers[5]:

?UPPER JOHN DAY

Oreodontoides (Paroreodon) stocki (1947, p. 257)
Promerycochoerus latidens (1949, p. 102)
P. (Parapromerycochoerus) macrostegus (1949, p. 118)
P. (Pseudopromerycochoerus) inflatus (1949, p. 123)
Desmatochoerus leidyi (1954, p. 185)
Superdesmatochoerus lulli (1954, p. 215)
Pseudogenetochoerus covensis (this paper, p. 161)
Eporeodon davisi (this paper, p. 203)
E. (Paraeporeodon) longifrons (this paper, p. 207)
Dayohyus wortmani (this paper, p. 217)

?MIDDLE JOHN DAY

Oreodontoides oregonensis (1947, p. 251)
O. (Paroreodon) marshi (1947, p. 256)
Promerycochoerus superbus (1949, p. 121)
P. (Parapromerycochoerus) macrostegus furlongi (1947, p. 121)
Desmatochoerus curvidens (1954, p. 182)
Superdesmatochoerus microcephalus (1954, p. 215)
Pseudogenetochoerus condoni (this paper, p. 159)
Eporeodon occidentalis (this paper, p. 201)
E. (Paraeporeodon) pacificus (this paper, p. 205)
Dayohyus trigonocephalus (this paper, p. 216)

[5] References are to papers by Schultz and Falkenbach.

JOHN DAY (?MIDDLE OR ?UPPER)

Promerycochoerus superbus chelydra (1949, p. 111)
Hypsiops johndayensis (1950, p. 123)
Pseudodesmatochoerus wascoensis (1954, p. 210)
Epigenetochoerus parvus (this paper, p. 164)
Eporeodon (Paraeporeodon) perbullatus (this paper, p. 210)
E. (P.) leptacanthus (this paper, p. 213)

Of the 19 forms listed under the genus *Eporeodon* by Thorpe,[1] only one (and a new species) is here recognized as *Eporeodon*, and three species and one subspecies are recognized under *Eporeodon* (*Paraeporeodon*), new subgenus. The following list indicates under what genus or subgenus these various forms can be found in papers by Schultz and Falkenbach:

"E." bullatus = *Otionohyus (Otarohyus) bullatus* (p. 118)
"E." condoni = *Pseudogenetochoerus condoni* (p. 159)
"E." dickinsonensis = *Genetochoerus (Osbornohyus) dickinsonensis* (p. 154)
"E." helenae = *Otionohyus (Otarohyus) hybridus helenae* (p. 131)
E. leptacanthus = *Eporeodon (Paraeporeodon) leptacanthus* (p. 213)
E. longifrons = *E. (P.) longifrons* (p. 207)
E. longifrons perbullatus = *E.* (*P.*) *l. perbullatus* (p. 210)
"E." major = *Paramerycoidodon (Barbourochoerus) major* (p. 92)
"E." major cedrensis = *Otionohyus (Otarohyus) cedrensis* (p. 127)
"E." major cheeki = *Mesoreodon cheeki* (1949, p. 135)
"E." major hybridus = *Otionohyus (Otarohyus) hybridus* (p. 129)
"E." major relictus = *Paramerychyus relictus* (1947, p. 249)
"E." montanus = *Subdesmatochoerus montanus* (1954, p. 219)
E. occidentalis = *Eporeodon occidentalis* (p. 201)
E. pacificus = *E. (Paraeporeodon) pacificus* (p. 205)
"E." parvus = *Epigenetochoerus parvus* (p. 164)
"E." socialis = *Subdesmatochoerus socialis* (1954, p. 220)
"E." thurstoni = *?Desmatochoerus (Paradesmatochoerus) thurstoni* (1954, p. 202)
"E." trigonocephalus = *Dayohyus trigonocephalus* (p. 216)

[1] 1937, p. x.

Simpson[2] considered the genus *Eporeodon* as belonging to the Merycoidodontinae with a range of "M. [Middle] Olig–L. [Lower] Mioc."

The present writers agree with Simpson that *Eucrotaphus* should be considered a *nomen vanum*. They do not agree, however, that there is any evidence that *Eporeodon* is synonymous with *Eucrotaphus*. The bullae of *Eporeodon* are distinct in that they are large and long vertically, whereas in *Eucrotaphus* the bullae are comparatively small and short vertically. These latter characteristics are more like those of some of the Oligocene [White River] forms, which appear to be unrelated to *Eporeodon*.

The foregoing list of species and subspecies attributed to the genus *Eporeodon* contains many kinds of oreodonts from the Great Plains region. The latter forms are chiefly from the Oligocene deposits, except for *"E." major relictus* from the Harrison and *"E." major cheeki* and *"E." thurstoni* from the Gering or from sediments of equivalent age.

The examples of *Eporeodon* have robust skulls but possess comparatively light teeth. The bullae are well inflated but are long and rather narrow (conical). There is a difference in size between *E. occidentalis* (presumably from the middle John Day) and the larger *E. davisi* (presumably upper John Day). These two species are considered to be in the same phylogenetic line.

Of those areas producing varied oreodont faunas, the John Day region is the only one that neither of the writers has seen. Collecting in a region should give one a much more comprehensive approach to the geologic problems of an area. Most of the earlier collections from the John Day lack geological field data, but some of the specimens collected later have been documented. Until an oreodont collection is available which has well-documented stratigraphic field data, it is difficult to establish any phylogenetic sequences of the John Day oreodonts. Morton Green[3] of the University of California agreed with the present writers concerning the value of geologic data associated with John Day oreodonts, when he reported, "Most of the mammalian specimens are of

[2] 1945, p. 149.
[3] 1950.

little or no value in correlating these beds since most of the materials are not accompanied by accurate stratigraphic data." It seems reasonable, however, to postulate sequences of phylogenetic lines similar to those stratigraphically documented by geological evidence from the Great Plains. The writers realize that this approach in regard to the John Day oreodonts is hypothetical, but it is based primarily on the morphologic characters. Of course, the writers assume that the trends in development in the John Day region are similar to those found in the Great Plains.

Douglass[1] discussed the genus *Eporeodon* and based his conclusion on the holotype of *E. occidentalis.* He stated, "The paroccipital processes are transverse and moderately expanded laterally and are not so prismatic behind the bullae as in *Eucrotaphus.*"

Thorpe's[2] illustration and a cast of the type specimen, Y.P.M. 10142, show that the paroccipital process was broken off near its base. The process is laterally expanded at its base, but other examples of both *E. occidentalis* and *E. davisi* suggest that the lower portion of the process is rounded.

Neither Marsh, Douglass, nor Thorpe mentioned the center protuberance on the frontals of the holotype (also on referred specimens). This particular character is also noticeable in the Desmatochoerinae.[3] Marsh,[4] in his original description, described the metacarpals, navicular, cuboid, and phalanges. Thorpe[5] quoted Marsh concerning the foot elements but did not mention the catalogue number of the particular specimen. The present writers have not found complete metatarsals, metacarpals, or portions of the feet that are associated with a single skull referable to this genus.

The examples of *Dayohyus,* in general appearances, are similar to those of *Eporeodon.* The major differences between the two genera are that in *Eporeodon* there are a more compressed, conical-shaped auditory bulla, a large and deep lacrimal fossa, and a protuberance on the midline of the frontal.

Distribution

Two species of *Eporeodon* are known from the lower Miocene (middle and upper John Day = Harrison in part) of Oregon. (See geologic distribution chart, p. 22.)

The assumed phylogenetic sequence of *Eporeodon* is as follows: *E. occidentalis* from the middle John Day and *E. davisi* from the upper John Day.

Summary of Species and Types

Two species of *Eporeodon* from one lower Miocene locality are here recorded:

1. *Eporeodon occidentalis* Marsh, from John Day Valley, Oregon. (?Middle John Day = approximate Harrison equivalent.)

Holotype: Skull, Y.P.M. 10142. Figures 24, 52.

2. *Eporeodon davisi,* new species, from John Day Valley, Oregon. (?Upper John Day = approximate Harrison equivalent.)

Holotype: Skull, A.M. 7576. Figure 24.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

EPOREODON

Total available specimens: 13

1. Eporeodon occidentalis Marsh

From questionably middle John Day (approximately equal to the Harrison of the Great Plains), John Day Valley, Oregon

Oreodon occidentalis Marsh, 1873, p. 409.

Eporeodon occidentalis: Marsh, 1875, p. 249; 1884, figs. 73, 162, 163. Thorpe, 1937, p. 81, figs. 41–43.

Eucrotaphus occidentalis (Marsh): Cope, 1879a, p. 59.

Characters

Skull: Smallest of genus. (See generic characters.)

Mandible: Smaller than examples of *E. davisi;* less abrupt downward curve to inferior border than in *E. davisi.* (See generic characters.)

[1] 1906, p. 565.
[2] 1937, fig. 42.
[3] Schultz and Falkenbach, 1954.
[4] 1873, p. 410.
[5] 1937, p. 83.

DENTITION: Series actually smaller than examples of *E. davisi,* proportionately (to length of skull) larger than mentioned species. (See generic characters.)

LIMBS: Smaller and lighter than those of *E. davisi.* (See generic characters.)

MEASUREMENTS: Tables 8 and 9 (pp. 196 and 198).

ILLUSTRATIONS: Figures 24, 30, 52.

DISCUSSION

The species *Eporeodon occidentalis* has a varied history. In addition to the foregoing references, the following conclusions have been reported:

Cope[1] considered the species a synonym of *Eucrotaphus jacksoni.* Trouessart[2] came to the same conclusion but later[3] considered it as *Eporeodon occidentalis.*

The examples of this species (and genus) are unique in that the skulls are very robust and low. There is a noticeable protuberance on the frontal at the midline, a long and narrow bulla, and the teeth are very light. The frontal protuberance is similar to those found in many skulls of the Desmatochoerinae[4] which are comparatively long and narrow. The somewhat brachycephalic skulls of *E. occidentalis* approach those of *Mesoreodon*[5] in general appearance but differ in their considerably lighter teeth and longer and narrower bulla. The light teeth approach those of *Genetochoerus* and *G.* (*Osbornohyus*), but the skull is much more robust. Actually, examples of *E. occidentalis* seem to possess characters of three unrelated phyla, the Desmatochoerinae, *Mesoreodon,* and *Genetochoerus.*

It is not known if the remains of *E. occidentalis* occurred in the middle or upper John Day. However, it is here presumed that they came from the middle and gave rise to those of *E. davisi* from the upper John Day.

Matthew,[6] in a discussion of oreodonts from eastern Colorado, wrote of "*E. occidentalis,* as [being] represented by some twenty cleaned skulls and three or four incomplete skeletons from the John Day region in the Cope collection." The present authors, however, found only three specimens in the American Museum collection that are referable to *E. occidentalis.*

Seven specimens are here recorded:

HOLOTYPE

Partial skull with P^2–P^3 alv. and P^4–M^3. (w)	Y.P.M. 10142	From ?middle John Day, Bridge Creek?, John Day River, Oregon; collected by L. S. Davis, 1874 Figured by Thorpe, 1921c, figs. 1–3· 1937, figs. 41–43 This report, figures 24, 52

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM TURTLE COVE:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Posterior portion of skull (lacking dentition), partial mandible (lacking dentition), partial scapula, partial humerus, partial radius, partial ulna, astragalus, calcaneum, fragments of manus and pes, and partial pelvis. Figure 30	A.M. 7661

The above specimen (collected by William Day, 1878) is not complete enough for definite identification.

3 SKULLS AND MANDIBULAR RAMI

Partial skull with C/–dP^2–M^2 and partial mandible with /C–dP_2–M_2 . . . . . . (I)	7585

The above specimen was collected by C. H. Sternberg, 1879.

[1] 1884b, p. 517.
[2] 1898, p. 836.
[3] 1905, p. 688.
[4] Schultz and Falkenbach, 1954.
[5] *Idem,* 1949.
[6] 1901, p. 396.

Partial skull with C/(br.)–M^3 (M^1–M^3 br.) and mandible with I_3–/C alv. and P_1–M_3	(w)	Y.P.M. 11024
The above specimen was collected by William Day, 1878.		
Skull with C/–dP^4–M^3(germ) (P^3 br.) and partial right ramus with M_1–M_3(br.) . .	(I)	11026

FROM HAY STACK VALLEY:

SKULL

Partial skull with P^2–M^3	(w+)	11053
The above two specimens were collected by L. S. Davis, 1875.		

FROM GENERAL AREA:

SKULL AND MANDIBLE (ATTACHED)

	U.C.
Partial skull and partial mandible (embedded in plaster)	1305

2. **Eporeodon davisi**,[1] new species

From questionably upper John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

DESCRIPTION

SKULL: Larger than examples of *E. occidentalis.* (See generic description.)

MANDIBLE: Larger than examples of *E. occidentalis;* sharper downward curve to inferior border posterior to M_3. (See generic description.)

DENTITION: Within size range of *E. occidentalis.* (See generic description.)

LIMBS: Slightly longer and slightly heavier than those of *E. occidentalis.* (See generic characters.)

MEASUREMENTS: Tables 8 and 9 (pp. 196 and 198).

ILLUSTRATIONS: Figures 24, 30, 52.

DISCUSSION

The new species *Eporeodon davisi* has a skull with a considerably longer basal length than that of *E. occidentalis.* The dentition, however, is not noticeably larger than that of *E. occidentalis.* It is here considered that examples of *E. davisi* occur in the upper John Day and were derived from examples of *E. occidentalis* from the middle John Day.

As previously mentioned, very little of the various John Day collections have definite field data, so the apparent geologic sequence is presumed on the basis of size changes of the skulls, which seem to be beyond the range of individual variation. In the *Eporeodon* material a marked size difference in the over-all length of the skulls is apparent, but little change, if any, is noted in the dentition. Actually, examples of *E. occidentalis* have proportionately larger tooth rows than those of *E. davisi,* which have larger skulls.

Six specimens are here recorded:

HOLOTYPE

Partial skull with P^2(rt.)–M^3. (w‡)	A.M. 7576	From the "Cove," ?upper John Day, (=Turtle Cove), John Day Valley, Oregon; collected by L. S. Davis, 1879 Figure 24

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

SKULL AND MANDIBLE

		A.M.
Partial skull with P^2–M^3 and partial mandible with P_2–M_3	(w‡)	7701

SKULL AND SKELETAL ELEMENTS

Partial skull with P^2–M^2(br.), tibia and astragalus. Figure 30	(w+)	7614
Included under A.M. 7614 is a partial right ramus with M_1–M_2 which suggests *Desmatochoerus*.		

[1] Named in honor of L. S. Davis who collected in the John Day area of Oregon.

FROM NORTH FORK:

SKULL		A.M.
Partial skull with P^3–M^1 rt. and M^2–M^3. Figure 52	(w)	7622

The measurements of the molars of the above skull are longer than in the type.
Collected by J. L. Wortman, 1879.

MAXILLA AND MANDIBLE		
Partial right maxilla with P^4–M^3(br.)	(w‡+)	7689
Partial mandible with I_1–I_2 alv. and I_3–M_3 (P_2 alv.) Figure 24	(–M)	7689

The above two specimens included under A.M. 7689 represent two different individuals. Also included is a partial tibia which is too large for either dentition.
Collected by L. S. Davis, 1879.

IA. EPOREODON (PARAEPOREODON), NEW SUBGENUS

SUBGENOTYPE: *Eporeodon* (*Paraeporeodon*) *longifrons* (Cope).

DESCRIPTION

SKULL: Medium in size; basal length ranging from 208 to 228 mm., widths from 130 to 145 mm.; dolichocephalic-mesocephalic; facial region moderately high, higher than examples of *Eporeodon;* supraoccipital wings moderately spread, more so than in those of *Eporeodon;* sagittal crest prominent but moderately light, more so than in examples of *Eporeodon;* frontal wide, lacking midline protuberance as in *Eporeodon;* supraorbital foramen with noticeable anterior groove; nasals narrow to wide, posterior border acute, more so than those of *Eporeodon;* anterior nasal-maxilla contact in area above P^1; orbit medium to large in size, looking mostly outward and upward, slightly forward; zygomatic arch moderately light; infraorbital foramen above posterior portion of P^3; lacrimal fossa large and deep, larger than in examples of *Eporeodon;* paroccipital process moderately light to moderately heavy; bulla well inflated, bulbous in outline; postglenoid process robust, peg-shaped to laterally expanded; posterior palate projecting posteriorly beyond M^3.

MANDIBLE: Light; postsymphysis below P_3; ramus shallow, deepening posteriorly; inferior border of ramus straight to a point below posterior portion of M_3, then a sharp downward curve; condyle set with internal border higher than external.

DENTITION: Light, but more robust than in examples of *Eporeodon;* external styles of molars prominent; P^1–P^3 each with moderately prominent anterior intermediate crest.

LIMBS: Moderately long; moderately robust; longer and more robust than examples of *Eporeodon.*

MEASUREMENTS: Tables 8, 9 (pp. 196 and 198).

ILLUSTRATIONS: Figures 25–27, 52 (skulls, mandibles, and dentitions), 30 (limbs).

DISCUSSION

The new subgenus *Eporeodon* (*Paraeporeodon*) includes forms with skulls that are larger than examples of *Eporeodon.* The latter also has a prominent midline protuberance on the frontals which is lacking, or nearly so, in the subgenus. The skulls are of light construction, but the dentition is slightly more robust than in examples of *Eporeodon.*

As in all the John Day oreodont material, the portion (middle or upper) of the John Day deposits, where cited, in many instances is assumed by the writers. Also, in cases in which skeletal material is associated under the same catalogue number as a skull, it may well be questioned that only one individual is represented (see discussion, p. 199).

DISTRIBUTION

Three species and one subspecies of *Eporeodon* (*Paraeporeodon*) are known from lower Miocene (middle and upper John Day = Harrison in part) of Oregon. (See geologic distribution chart, p. 22.)

The assumed sequence of *E.* (*Paraeporeodon*) is as follows: *E.* (*P.*) *pacificus* from middle John Day; *E.* (*P.*) *longifrons* from upper John Day; *E.* (*P.*) *l. perbullatus* and *E.* (*P.*) *leptacanthus* may occur in either the upper or middle John Day, as they do not suggest a vertical sequence (based on material at hand).

Summary of Species and Types

Three species and a subspecies of *Eporeodon* (*Paraeporeodon*) from one lower Miocene locality are here recorded:

1. *Eporeodon* (*Paraeporeodon*) *pacificus* (Cope), from John Day Valley, Oregon. (?Middle John Day = approximate Harrison equivalent.)

Holotype: Skull, A.M. 7502. Figures 25, 26.

2. *Eporeodon* (*Paraeporeodon*) *longifrons* (Cope), from John Day Valley, Oregon. (?Upper John Day = approximate Harrison equivalent.)

Holotype: Skull, A.M. 7504. Figure 26.

2a. *Eporeodon* (*Paraeporeodon*) *longifrons perbullatus* (Thorpe), from John Day Valley, Oregon. (John Day = approximate Harrison equivalent.)

Holotype: Skull and mandible, Y.P.M. 11011.

3. *Eporeodon* (*Paraeporeodon*) *leptacanthus* (Cope), from John Day Valley, Oregon. (John Day = approximate Harrison equivalent.)

Holotype: Skull, A.M. 7695. Figures 25–27.

DETAILED LIST OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

EPOREODON (PARAEPOREODON)

Total available specimens: 94

1. Eporeodon (Paraeporeodon) pacificus (Cope)

From questionably middle John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eucrotaphus jacksoni pacificus Cope, 1884a, p. 518.

Eucrotaphus pacificus (Cope): Trouessart, 1898, p. 836.

Eporeodon occidentalis pacificus (Cope): Matthew, 1899b, p. 64.

Eporeodon pacificus (Cope): Hay, 1902, p. 667. Thorpe, 1937, p. 83, pl. 8, figs. 1–3.

Eporeodon leptacanthus pacificus (Cope): Thorpe, 1921c, p. 95.

Eporeodon bullatus (Leidy), in part: Thorpe, 1937, p. 65, figs. 28–30.

Characters

Skull: Mesocephalic; slightly smaller than examples of *E.* (*P.*) *longifrons* and *E.* (*P.*) *l. perbullatus;* tendency for supraorbital foramina to be close together in *E.* (*P.*) *longifrons,* slight groove extending anteriorly from supraorbital foramen to a point on side of face in area above P^2, less prominent than in examples of *E.* (*P.*) *longifrons;* orbit moderately large; nasals usually narrow compared with those of *E.* (*P.*) *longifrons,* more anterior retraction than in *E.* (*P.*) *leptacanthus;* bulla smallest of subgenus; paroccipital process wide laterally, tapering below transversely, oblong in outline; postglenoid process moderately expanded laterally; less posterior extension of palate than in examples of *E.* (*P.*) *longifrons.*

Mandible: Lighter in structure than examples of *E.* (*P.*) *longifrons.*

Dentition: (See subgeneric description).

Limbs: (See subgeneric description).

Measurements: Tables 8 and 9 (pp. 196 and 198).

Illustrations: Figures 25–27, 30, 52.

Discussion

Examples of *Eporeodon* (*Paraeporeodon*) *pacificus* indicate that this form is the middle John Day representative of a phylogenetic line, with *E.* (*P.*) *longifrons* the probable upper John Day species.

It should be noted that the holotype of *E.* (*P.*) *longifrons* is somewhat crushed (see discussion, p. 208). The orbit of the holotype of *E.* (*P.*) *pacificus* is larger than the figured specimen (A.M. 7591) of *E.* (*P.*) *longifrons.*

Both Cope[1] and Thorpe[2] made comparisons between *E.* (*P.*) *pacificus* and *Paramerycoidodon* (*Barbourochoerus*) *major.* The holotype of *major* is a maxilla with comparatively robust dentition from the Oligocene deposits of the Great Plains. Many of the early comparisons were made between forms from the John Day and those of the Great Plains Oligocene. As stated elsewhere, no forms referable to the Eporeodontinae are generically the same as any from the Great Plains.

Twenty-five specimens are here recorded:

[1] 1884a, p. 219.
[2] 1937, p. 83.

HOLOTYPE

Skull with I^1–I^3 rt. and C/–M^3. (w‡)	A.M. 7502	From ?upper John Day, John Day Valley, Oregon Figured by Thorpe, 1937, pl. 8, figs. 1–3 This report figures, 25, 26

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM THE "COVE":

SKULL AND MANDIBLE — A.M.

Skull with I^2–M^3 and mandible with I_1–M_3. Figure 52 . . . . (w) 7777

The above specimen (collected by L. S. Davis, 1879) approaches examples of *E. (P.) leptacanthus.*

Posterior portion of skull with M^2(br.)–M^3 . . . . (w) 7542

Associated under the above number are a partial femur and partial tibia which seem referable to *Promerycochoerus*. The above specimen was collected by J. L. Wortman, 1878.

Partial skull with I^1–C/ and P^1–M^3, partial femur, partial tibia (small size), partial astragalus (small size), partial pes, and fragments . . . . (w) 7786

The above specimen was collected by Warfield and Day, 1877.

3 SKULLS

Skull with I^1(alv.)–M^3 (1877) . . . . (w+) 7632

Partial skull with C/(rt.)–M^3 (P^1 rt.) . . . . (w) 7714

The above specimens were collected by J. L. Wortman, 1879.

Y.P.M.

Partial skull with C/–M^3 . . . . (w) 10146

The above specimen was designated a plesiotype of *Eporeodon bullatus* (=*Otionohyus* (*Otarohyus*) *bullatus*) by Thorpe, 1937. The specimen was collected by William Day, 1875.

MANDIBLE AND SKELETAL ELEMENTS

A.M.

Mandible with I_1(alv.)–M_3 (I_2 rt.), 2 humeri, partial radius, partial ulna, partial manus, 2 femora (1 partial), 2 tibiae, partial pes, 2 astragali, 2 partial calcanea, partial pelvis and vertebrae. Figure 30 . . . . (w+) 7783

The above specimen was collected by J. L. Wortman, 1879.

FROM CAMP CREEK, CROOKED RIVER (COLLECTED BY J. L. WORTMAN, 1879):

SKULL AND SKELETAL ELEMENTS

Skull with I^2(alv.)–M^3, humerus, partial ulna, 2 astragali, and vertebrae . . . . . (w‡) 7499

Under the above number are two partial humeri and a partial radius of a smaller oreodont.

2 SKULLS

Posterior portion of skull with P^4(rt.)–M^3 (1879) . . . . (w‡+) 7658

Partial skull with dP^3–M^3(erupt.), and vertebrae (1879) . . . . (I) 7874

FROM THE "COVE" (COLLECTED BY DAY AND WARFIELD, 1877):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Anterior portion of skull with I^1(rt.)–M^3(br.) (P^1–P^2 rt.), partial mandible with /C–P_2 rt. and P_3(br.)–M_3(br.), ball of femur, and partial tibia . . . . (w‡+) 7880

FROM ALAMO RANCH, JOHN DAY RIVER:

SKULL

Partial skull with C/–M^3. . . . . (w+) 7616

FROM BRIDGE CREEK (COLLECTED BY L. S. DAVIS, 1874):

SKULL		Y.P.M.
Partial skull with I^1–I^3 rt. and $C/$–M^3	(W)	12299
The above skull was considered by Thorpe, 1937, a plesiotype of *Eporeodon bullatus* [=*Otionohyus* (*Otarohyus*) *bullatus*]. Figured by Thorpe, 1937, figs. 28–30.		

FROM U.C. COLL. LOC. NO. 898 (COLLECTED BY DAVIS AND OSMONT, 1900):

SKULL		U.C.
Partial skull with I^2–I^3 rt. and $C/$–M^3	(M+)	1912

FROM THE NORTH FORK (COLLECTED BY L. S. DAVIS, 1875):

2 SKULLS		Y.P.M.
Partial skull with C/M^3 (P^2 erupt.)	(−M)	12401
Partial skull with $C/$–M^3.	(W)	12404

FROM GENERAL AREA:

3 SKULLS AND MANDIBULAR RAMI		A.M.
Partial skull with I^1–M^3 and partial mandible (attached) with I_1–M_3(br.)	(W)	7556
Skull with I^1–M^3 and mandible with I_1–M_3. Figure 27 (in part)	(W)	7557
Partial skull with C/dP^4(erupt.), partial right ramus with M_2(br.)–M_3(erupt.), fragment of scapula, and fragment of pelvis	(I)	7821

2 SKULLS AND SKELETAL ELEMENTS		
Partial skull with I^1–M^3 (P^1–P^3 rt.), partial humerus, partial radius, and partial ulna	(W‡‡)	Y.P.M. 12402
Partial skull with C/P^1 rt. and P^2–M^3, partial humerus, partial radius, partial ulna, partial femur, and fragments	(W)	A.M. 7779
The partial femur is lighter than that of A.M. 7783.		

MANDIBLE AND SKELETAL ELEMENTS		
Partial mandible with P_1(alv.)–M_3, femur, tibia, astragalus, partial calcaneum, partial pes, partial pelvis, vertebrae, and fragments	(W+)	7866

2 SKULLS		U.O.
Partial skull with I^1–I^3 rt. and $C/$(br.)–M^3	(W+)	F676
The above specimen was collected by Thomas Condon.		A.M.
Skull with I^1–I^3 rt. and $C/$(br.)–M^3	(W)	7626

2. **Eporeodon (Paraeporeodon) longifrons** (Cope)

From questionably upper John Day deposits (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eucrotaphus major longifrons COPE, 1884a, p. 519.

Eporeodon major longifrons (Cope): MATTHEW, 1899b, p. 64.

Eporeodon longifrons (Cope): HAY, 1902, p. 667. THORPE, 1937, p. 71, pl. 5, figs. 1–3.

CHARACTERS

SKULL: Mesocephalic, larger than examples of *E.* (*P.*) *pacificus;* sagittal crest more prominent and higher posteriorly than in mentioned species; supraorbital foramina farther apart, with a more noticeable anterior and inward groove than in examples of *E.* (*P.*) *pacificus;* nasals wide, tending to extend posteriorly for longer distance than in above species, with more noticeable anterior retraction than in examples of *E.* (*P.*) *leptacanthus;* paroccipital process wide at base, tapering rapidly to a rounded, inferior portion [more oblong in *E.* (*P.*) *pacificus*]; bulla well inflated, more so than in examples of last-mentioned species; postglenoid process wide laterally; palate extended posteriorly for noticeable distance posterior to M^3.

MANDIBLE: Moderately robust, more robust and deeper than examples of *E.* (*P.*) *pacificus*;

condyle wider transversely.

DENTITION: (See subgeneric description).

LIMBS: Approximately equal to those of examples of *E.* (*P.*) *pacificus*.

MEASUREMENTS: Tables 8 and 9 (pp. 196 and 198).

ILLUSTRATIONS: Figures 25–27, 30, 52.

DISCUSSION

Cope[1] originally considered this form a subspecies of *"Eucrotaphus major"* [= *Paramerycoidodon* (*Barbourochoerus*) *major*, this report, p. 92] and stated: "Known from a single skull from the North Fork of the John Day River, Oregon . . . It may be observed here that the Oreodontidae of this locality are mostly distinct from the species of the John Day River proper." Thorpe[2] stated, "Data in the American Museum, however, indicates that the type was collected at 'The Cove,' which is not on the North Fork." According to Matthew's[3] list, the holotype, A.M. 7504, did come from the "Cove."

Actually Cope gave no description of his subspecies, and it remained undescribed until Thorpe's report. Thorpe also based the mandibular characters on Y.P.M. 11020, which is associated with a skull that is also here referred to the same species.

The holotype skull, A.M. 7504, is badly crushed, especially in the area of the muzzle. At first it was thought that the muzzle lacked contact with the rest of the skull. However, close examination shows a perfect contact. (The skull is crushed and the muzzle appears to be elongated.)

The zygomatic arches are absent, and the dentition in a poor stage of preservation in the holotype. A well-preserved skull and mandible, A.M. 7591 (figs. 25, 27, 30) is here illustrated with the type. The outstanding difference between the two is noted in the muzzle area.

The examples of *E.* (*P.*) *longiceps* from the ?upper John Day suggest that this species is in the same phylogenetic line as *E.* (*P.*) *pacificus*. The size range between the two forms is approximately the same as recognized in the *Eporeodon* phylum also from the John Day. It should also be noted that the size range is similar to that found in certain phyla in the Great Plains, where the geologic evidence is well known.

Twenty-eight specimens are here recorded:

HOLOTYPE

Partial skull with I^2–I^2 alv. and I^3(br.)–M^3(br.) (P^1–P^2 rt. and M^1–M^2 br.). (w+)	A.M. 7504	From the "Cove," ?upper John Day, John Day Valley, Oregon; collected by C. H. Sternberg, 1879 Figured by Thorpe, 1937, pl. 5, figs. 1–3 This report, figure 26

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM THE ALAMO RANCH, JOHN DAY RIVER:

2 SKULLS AND MANDIBLES (ATTACHED)		A.M.
Partial skull with P^3–M^3 and partial mandible with P_4–M_3	(w+)	7739
		Y.P.M.
Skull with I^1–M^3 and mandible (attached) with I_1–M_3 (not completely prepared) .	(?w)	11020
SKULL		
Posterior portion of skull with M^2–M^3(erupt.)	(–M)	7738

FROM TURTLE COVE (THE "COVE"):

3 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS		
Skull with I^1–I^3 rt. and C/(br.)–M^3 (P^1, P^3 and M^1 br.), anterior portion of mandible with I_1–/C rt. and P_1(br.)–P_4, partial pelvis, and vertebrae	(w+)	7500

[1] 1884a, p. 520.
[2] 1937, p. 71.
[3] Handwritten list of John Day Cope collection made by W. D. Matthew at the time of purchase of the collection.

The above specimen has a smaller over-all dental series than the other examples of this species. A.M.

Skull with I^1–M^3, axis and atlas. Figure 52 . . . . (w) 7567

The A. M. catalogue includes a mandible under A. M. 7567 but, at this time, it has not been found. Another skull with the same number is listed under *Pseudogenetochoerus covensis.*

Partial skull with I^1–M^3 and C/–M^3, mandible with I_1–/C alv. and P_1–M_3, partial scapula, vertebrae, and fragments . . . . (w+) 7900

The above number has also been used for some loose teeth.

SKULL AND MANDIBLE

Anterior portion of skull with I^1(alv.)–M^3 and partial mandible (attached) with I_3(rt.)–M_3, (P_2 absent, lacking in life) . . . . (w‡) 7562

Another specimen, A.M. 7562, listed under *E. (P.) perbullatus.*

SKULL AND SKELETAL ELEMENTS

Posterior portion of skull with M^2–M^3 br., partial femur, partial tibia, partial pes, partial pelvis, and vertebrae . . . . (w‡) 7545

The above specimen was collected by J. L. Wortman, 1879.

SKULL AND MANDIBLE

Anterior portion of skull with dP^3–M^3, partial right ramus with P_4(erupt.)–M_3(br.) (M_1 rt.) . . . . (I) 7445

The above two skulls are associated under the same A.M. number. Matthew's original listing of the Cope collection gives the data for the first listed specimen. The location of the second specimen is questionable.

4 SKULLS

Partial skull with C/–M^3 (P^1 br.) . . . . (w) 7521

The above specimen was collected by William Day, 1878.

Anterior portion of skull with I^1–I^3 alv. and C/(rt.)–P^4 (P^1 rt.) . . . . (w‡) 7619

Posterior portion of skull with M^3 . . . . (w‡+) 7637

The above two specimens were collected by C. H. Sternberg, 1879.

Partial skull with I^1–I^3 alv. and C/(br.)–M^3 . . . . (M+) 7882

The above specimen was collected by J. L. Wortman, 1879.

FROM CAMP CREEK (COLLECTED BY J. L. WORTMAN, 1879):

SKULL

Skull with I^3–M^3 . . . . (w‡+) 7496

FROM C.I.T. COLL. LOC. NO. 8 (C.I.T. CATALOGUE RECORDS THIS LOCALITY AS "MIDDLE" JOHN DAY):

SKULL AND MANDIBLE

Posterior portion of skull with M^1–M^3 and partial mandible with I_1–I_3 rt. and /C(br.) (P_1–P_2 br.) . . . . (M) C.I.T. 515

SKULL AND SKELETAL ELEMENTS

Anterior portion of skull with I^1–M^3 (I^3 rt., C/ and P^2 br.), two partial humeri, partial radius, partial femur, partial tibia, and astragalus . . . . (w+) 514

FROM C.I.T. COLL. LOC. NO. 241 (NEAR MONUMENT):

SKULL AND MANDIBULAR RAMUS, IMMATURE

Partial skull with C/(br.)–dP^4–M^3(erupt.) (P^2–P^3 alv.) and partial left ramus with I_1(erupt.)–M_3 (/C–P_1 alv., P_2 rt. and P_3–P_4 absent) . . . . (I) 1787

FROM C.I.T. COLL. LOC. NO. 136 (NORTH OF HUMPHREY'S RANCH):

SKULL — C.I.T.

Partial skull with P^2–M^3 . . . . (w‡) 511

FROM C.I.T. COLL. LOC. NO. 246 (EAST OF MONUMENT):

SKULL

Partial skull with P^3(br.)–M^3 . . . . (w) 1788

FROM U.C. COLL. LOC. NO. 869 (RUDIO CREEK):

SKULL — U.C.

Partial skull with C/(br.)–M^3 (P^2alv.) . . . . (M+) 1281

FROM NORTH FORK, JOHN DAY RIVER (COLLECTED BY THOMAS CONDON):

SKULL AND MANDIBLE (ATTACHED) — U.O.

Skull and mandible F666

FROM GENERAL AREA:

2 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Skull with I^1–I^2 rt. and I^3–M^3, mandible with I_1–M_3, femur, partial tibia, astragalus, calcaneum, pelvis, and vertebrae. Figures 25–27, 30 (in part) . . . . (w‡ +) A.M. 7591

Partial skull (with questionable contact between anterior and posterior portions) with C/–P^2(rt.) and P^3–M^3 (P^4–M^1 rt.), partial symphysis with I_1–/C, two partial femora, partial tibia, partial astragalus, vertebrae, and fragments . . . . (w) 7629

Also included in above number are two phalanges and a partial tibia of a horse.

SKULL AND SKELETAL ELEMENTS

Partial skull with P^2(rt.)–M^3, and partial humerus . . . . (w‡) 7555

The above humerus is lighter than other limb elements referred to this species.

2 SKULLS

Crushed partial skull with C/–M^3(br.) (P^1 rt.) . . . . (M) 7528

Partial skull with I^1–I^3 alv. and C/(rt.)–M^3. . . . . (w‡) U.C. 92

MANDIBLE AND SKELETAL ELEMENTS — A.M.

Partial mandible with I_1(rt.)–M_3(br.) (P_1 br.), and partial metapodials . . . . . (M+) 7645

2a. **Eporeodon (Paraeporeodon) longifrons perbullatus** (Thorpe)

From John Day deposits (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eporeodon perbullatus THORPE, 1921c, p. 106, figs. 9, 10.

Eporeodon longifrons perbullatus THORPE, 1937, p. 72, figs. 35–37.

CHARACTERS

SKULL: Mesocephalic to subbrachycephalic; tendency to be smaller than examples of species; sagittal crest (no example available with unbroken crest) questionably high but less so than in the species; supraorbital foramen with anterior groove; nasals moderately heavy, posterior border usually obtuse, extending posteriorly to just beyond anterior border of orbit; paroccipital process moderately wide and light at base; bulla bulbous, more expanded than in examples of *E.* (*P.*) *longifrons;* postglenoid process peg-shaped, almost as long anteroposteriorly as wide laterally; palate with less posterior extension beyond M^3 than in *E.* (*P.*) *longifrons.*

MANDIBLE: Smaller than that of *E.* (*P.*) *longifrons.*

DENTITION: Premolars more crowded than in species.

LIMBS: (See generic description).

MEASUREMENTS: Table 8 (p. 196).

ILLUSTRATIONS: Figures 25–27, 30.

DISCUSSION

Thorpe[1] described the bullae as "relatively enormous, full and ovate and nearly twice the

[1] 1921c, p. 106; 1937, p. 73.

size of those in *E. leptacanthus*." The present writers agree that the bulla is large but not twice the size of the bullae of *E.* (*P.*) *leptacanthus*. Thorpe[1] also stated, "Cat. Nos. 11011 and 12320 Y.P.M. are probably males while Cat. No. 12319 is more delicately proportioned and may well be a female."

The present writers have followed Thorpe in considering this form a subspecies of *longifrons*. As previously discussed, the geologic occurrence of many John Day examples is questionable. If it should be proved that the examples of this subspecies came from the middle John Day and those of *longiceps* came from the upper, they could well be in the same phylogenetic line. It is reasonable to expect that the forms here referred to *E.* (*Paraeporeodon*) may actually belong to two separate phylogenetic lines.

Twenty-four specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3 and mandible (attached) with I_1–M_3 rt. and /C–M_3. (w)	Y.P.M. 11011	From John Day deposits, Bridge Creek, John Day Valley, Oregon; collected by S. H. Snook, 1874 Figured by Thorpe, 1921c, figs. 9, 10; 1937, figs. 35–37

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM BRIDGE CREEK (COLLECTED BY L. S. DAVIS, 1874):

SKULL AND MANDIBLE (ATTACHED) — Y.P.M.

Skull with I^1–I^2 alv. and I^3–M^3, mandible with I_1–M_3, and limb bone fragments . (w) 12319

The above specimen was considered a paratype of this species by Thorpe, 1937.

SKULL

Partial skull with I^1–I^3 alv. and C/(rt.)–M^3 (P^1 rt.) . . . . (w+) 12320

The above specimen was considered as a paratype of this species by Thorpe, 1937.

FROM NORTH FORK OF JOHN DAY RIVER (COLLECTED BY L. S. DAVIS, 1875):

SKULL

Skull with C/(rt.)–M^3 (P^1 and M^1–M^3 br.) . . . . ($w\ddagger^+$) 12403

FROM NEAR C.I.T. COLL. LOC. NO. 3, NEAR CANT RANCH (C.I.T. CATALOGUE RECORDS THIS LOCALITY AS "MIDDLE" JOHN DAY):

SKULL — C.I.T.

Partial skull with I^1–I^2 alv. and I^3–M^3 . . . . (w) 505

FROM ALAMO RANCH:

SKULL — A.M.

Anterior portion of skull with C/–P^2 rt. and P^3–M^3 . . . . (w) 7736

FROM CAMP CREEK, CROOKED RIVER (COLLECTED BY J. L. WORTMAN, 1879):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Anterior portion of skull with C/(rt.)–M^3, partial mandible with M_1–M_3, astragalus and metapodial . . . . ($w\ddagger^+$) 7775

The above limb elements seem to be too small and light for this form.

[1] 1937, p. 74.

3 SKULLS A.M.

Partial skull with C/(br.)–M^3. . . . . (w) 7583
Partial skull with dP^3(br.)–M^2 . . . . (I) 7605
Inferior, anterior portion of skull with C/–P^1 rt. and P^2–M^3(br.) . . . . (w‡) 7662

FROM THE "COVE":

SKULL AND MANDIBLE

Skull with I^3–M^3, mandible with I_1–M_3 and vertebrae. Figures 25–27, 30 . . . . (w) 7497

The auditory bullae of the above skull are smaller than those of the holotype. A.M. 7497 bulla measures, anteroposteriorly, 23 mm., laterally, 18 mm., and the height is 22 mm.; that of the holotype, Y.P.M. 11011, anteroposteriorly, 31.5 mm., laterally, 23.5 mm., and the height is 28 mm.

Included under the above number are 2 partial femora, tibia (fig. 30), partial fibula, calcaneum, partial pes, and partial pelvis. These are partially embedded in green matrix and are possibly referable to *Epigenetochoerus parvus*. A posterior portion of a left ramus (lacking dentition) is also included under this number and the adhering grayish tan matrix is similar to that on the skull and mandible. (Compare V, fig. 22, and E, fig. 30.)

2 SKULLS AND MANDIBLES

Anterior portion of skull with C/–M^3(br.) (P^1 rt.), partial mandible with P_1–M_3(br.) (P_2 rt.), partial pelvis, and vertebrae . . . . (w) 7562

The above specimen was collected by C. H. Sternberg, 1879.

The dentition approaches examples of *E.* (*P.*) *leptacanthus*.

There is a second specimen with the above number but this is listed under *E.* (*P.*) *longifrons*.

The above skull approaches examples of *E.* (*Paraeporeodon*) *pacificus*.

Posterior portion of skull. 7584

2 SKULLS

Partial skull with I^1–I^3 alv. and C/(br.)–M^3 . . . . (w‡‡) 7495

The above three specimens were collected by L. S. Davis, 1879.

Anterior portion of skull with P^1(br.)–M^3(br.) . . . . (w‡+) 7782

The above speciman was collected by Day and Warfield, 1877.

FROM SHEEP MOUNTAIN, 1926 (C.I.T. CATALOGUE RECORDS HORIZON OF THIS SPECIMEN AS "MIDDLE" JOHN DAY):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull (in 2 pieces) with I^3–M^3(br.), partial mandible with /C(br.)–M_3(br.) (P_2 and P_4 br.), and 2 partial humeri . . . . (w+) C.I.T. 2689

FROM THE GENERAL AREA:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with C/(erupt.)–dP^2(br.)–M^2(germ), mandible (attached) with I_1–/C alv. and P_1(erupt.)–dP_3–M_1 (P_1 br.), partial scapula, partial humerus, astragalus, and atlas. . . . . (I) A.M. 7514

4 SKULLS AND MANDIBULAR RAMI

Skull (in two sections) with I^2–M^3 (I^3 alv. and P^2 rt.) . . . . (w) 7515
Partial mandible with I_1(rt.)–dP_3–M_2 (I_2–/C rt.) . . . . (I) 7515

The above two specimens are included under the same number.

Partial skull (in two sections) with I^2–P^2 rt. and P^3–M^3 br. and partial left ramus with M_2–M_3 br. . . . . (w) 7546
Partial skull (crushed) with C/(br.)–M^3 (P^1 rt.) and crushed mandible with I_2–/C rt. and P_1–M_3 (P_2 br.) . . . . (w+) 7830

SKULL AND SKELETAL ELEMENTS		A.M.
Partial skull with C/(br.)–M^3, partial humerus, and partial femur	(M+)	7487
The above skull is exceptionally long from orbit to supraoccipital wings.		

SKULL		U.O.
Partial skull with C/–P^4 rt. and M^1–M^3 br.	(W+)	682

3. Eporeodon (Paraeporeodon) leptacanthus (Cope)

From John Day deposits (approximately equal to the Harrison of the Great Plains), John Day Valley, Oregon

Eucrotaphus jacksoni leptacanthus Cope, 1884a, p. 519.

Eporeodon occidentalis leptacanthus (Cope): Merriam and Sinclair, 1907, p. 187.

Eporeodon leptacanthus (Cope): Matthew, 1909, p. 109. Thorpe, 1937, p. 71, pl. 5, figs. 1–3.

Characters

Skull: Dolichocephalic; sagittal crest moderately prominent, not so high as in examples of *E.* (*P.*) *longifrons,* more equal to crest in those of *E.* (*P.*) *l. perbullatus;* supraoccipital foramen with prominent anterior groove extending forward and inward; malar shallow below orbit, more so than in other examples of subgenus; nasals moderately light, posterior border subacute; paroccipital process wide at base, external surface almost parallel to anteroposterior axis of skull; bulla well inflated, longer anteroposteriorly than laterally; postglenoid process peg-shaped, similar to examples of *E.* (*P.*) *l. perbullatus;* posterior palate extends posteriorly to a point opposite the posterior border of M^3.

Mandible: Moderately light, lighter than in examples of *E.* (*P.*) *longiceps.* (See subgeneric description.)

Dentition: P^1–P^4 each with short but prominent anterior intermediate crests (right P^4 of holotype is abnormal in that the primary cusp has developed into a very prominent external style, see figs. 25 and 27); external styles very prominent on superior molars.

Limbs: (See subgeneric description).

Measurements: Tables 7 and 8 (pp. 146 and 196).

Illustrations: Figures 25–27, 30.

Discussion

Originally, Cope[1] considered this species a subspecies of *Eucrotaphus jacksoni.* This particular form, however, and *Paramerycoidodon* (*Barbourochoerus*) *major* (the basis of much of Cope's John Day oreodont comparisons), are both from the Great Plains. *Eucrotaphus jacksoni* is discussed on page 165, and considered a *nomen vanum,* since the holotype is the posterior portion of a skull, lacking dentition, and is indeterminable. It also should be noted that the holotype of *P.* (*B.*) *major* is a maxilla.

Cope[2] stated, "This [*E.* (*P.*) *leptacanthus*] is the largest form of the genus [*Eucrotaphus*], exceeding the typical *E. major* in the length of the skull by 23 mm." It is not known, however, what kind of skull he considered to be "the typical *E. major*" form. The present writers do not believe that there is a close relationship between any of the Eporeodontinae forms and species from the Oligocene of the Great Plains.

The examples of *E.* (*P.*) *leptacanthus* differ considerably from other forms of the subgenus, and enough variation is present to suggest another phylum. Actually, in general appearance, the skulls of this species are somewhat similar to examples of the Desmatochoerinae[3] but are smaller and possess a lighter dentition than the John Day forms of the same subfamily.

The holotype skull, A.M. 7695, is crushed but actually is the best-preserved example of all the referred material. The two skulls C.I.T. 506 and 2691 are wider than the others referred to this species, perhaps because they are also badly crushed.

Matthew's list of the Cope collection (see discussion, p. 193) includes a mandible with the holotype skull. To date, the associated mandible has not been found.

Seventeen specimens are here recorded:

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[1] 1884a, p. 519.
[2] 1884a, p. 519.
[3] Schultz and Falkenbach, 1954, pp. 182, 185.

HOLOTYPE

Skull with I^1(br.)–M^3 (Matthew's list also includes a mandible). (w)	A.M. 7695	From John Day deposits, John Day Valley, Oregon; collected by J. L. Wortman, 1879 Figured by Thorpe, 1937, pl. 5, figs. 1–3 This report, figures 25–27

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM THE "COVE":

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS — A.M.

Partial skull with C/–dP^3–M^3, mandible with P_1–dP_4–M_3, atlas, and fragments . . (I) 7503
The above specimen was collected by J. L. Wortman, 1879.
Partial skull with P^3–P^4 rt. and M^1(br.)–M^3, mandible with I_1–M_3 (/C absent and P_1 rt.) 2 humeri (1 partial), radius, ulna, femur, partial tibia, astragalus, calcaneum, and pelvis. Figures 27, 30 . . . . (w) 7694
The above specimen was collected by C. H. Sternberg, 1879.

SKULL, MANDIBLE, AND ATLAS

Partial skull with I^1–M^3, mandible with I_1–P_2 rt. and P_3–M_3, and atlas . . . . . (w) 7526
The above specimen was collected by Day and Warfield, 1877.

SKULL AND SKELETAL ELEMENTS

Posterior portion of skull (lacking dentition), partial humerus, partial ulna, femur, and vertebrae 7636

3 SKULLS

Partial skull with M^2–M^3 . . . . (M) 7544
Partial skull (in two sections) with C/(rt.)–dP^3–M^3 . . . . (I) 7570
The above three specimens were collected by C. H. Sternberg, 1878, 1879. Y.P.M.
Partial skull with P^3–M^3 . . . . (w) 12400
The above specimen was collected by William Day, 1875. Thorpe (1937, p. 75) referred this specimen to "*Eporeodon*" *major*.

FROM ALAMO RANCH:

SKULL

Partial skull with C/–M^3 . . . . (M) 7740

FROM JOHN DAY AREA:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P^4–M^3, fragments of mandible with P_3–P_4 and M_2–M_3, partial radius, vertebrae, and fragments . . . . (w) 7612

SKULL AND MANDIBLE (ATTACHED) — U.O.

Skull with I^1–M^3 and mandible with I_1–I_3 (not prepared). F681

FROM HAYSTACK VALLEY (COLLECTED BY WILLIAM DAY, 1876):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^2–M^3, mandible with I_1–I_3 rt. and /C–M_3, femur, 2 tibiae (one partial), partial pes, calcaneum, and fragments . . . . (w+) Y.P.M. 11007

FROM UNKNOWN LOCALITY:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^1(rt.)–M^3 (I^2–C/br.), partial mandible with M_3, and vertebrae . (w‡+) 12408
The above 2 specimens have the same field number.

FROM C.I.T. COLL. LOC. NO. 2, EAST OF CANT RANCH (C.I.T. CATALOGUE RECORDS THIS LOCALITY AS "MIDDLE" JOHN DAY):

SKULL, IMMATURE		C.I.T.
Partial skull with C/(br.)–dP^3–M^2(germ)	(I)	509

FROM C.I.T. COLL. LOC. NO. 4, NEAR CANT RANCH (C.I.T. CATALOGUE RECORDS THIS LOCALITY AS "MIDDLE" JOHN DAY):

SKULL		
Partial skull with I^3–M^3	(w‡‡)	506

FROM JOHN DAY AREA:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with C/M^3 and mandible with I$_1$–M$_3$	(w+)	2691

FROM U.C. COLL. LOC. NO. 873½ (J. NAYLONS), 1899:

SKULL		U.C.
Skull with I^1–I^3 alv. and C/M^3	(w)	1171

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

DAYOHYUS

TOTAL AVAILABLE SPECIMENS: 19

II. DAYOHYUS, NEW GENUS

GENOTYPE: *Dayohyus wortmani*, new species.

SKULL: Small to medium in size; basal lengths from 170 to 200 mm., widths from 125 to 152 mm.; mesocephalic to brachycephalic; low and flat; supraoccipital wings moderately expanded laterally, more so than in examples of *Eporeodon*, extending posteriorly for short distance posterior to condyles; brain case more depressed than in examples of *Eporeodon;* sagittal crest low; frontals wide, lacking midline protuberance as in *Eporeodon;* nasals wide, posterior border obtuse; nasal-maxilla contact in area posterior of C/ to anterior of P^1; supraorbital foramen with pronounced anterior groove; orbit medium to large, roundish, directed mostly outward, upward, and forward (more upward than in *Eporeodon*); zygomatic arch robust, more so than in *E.* (*Paraeporeodon*); infraorbital foramen above P^3; lacrimal fossa small, moderately deep, smaller and more shallow than in other genera of subfamily; muzzle broad; paroccipital process light; bulla well inflated; hyoidal groove present; postglenoid process robust, laterally expanded; posterior palate produced well beyond posterior border of M^3.

MANDIBLE: Ramus deeper posteriorly; ascending ramus moderately high, inferior border with noticeable inward curve.

DENTITION: Light, similar to examples of *Eporeodon*, lighter than in *E.* (*Paraeporeodon*); weak external styles on superior molars; P^1–P^3 each with light anterior intermediate crest.

LIMBS: As long as but lighter than examples of *Eporeodon*.

MEASUREMENTS: Tables 8 and 9 (pp. 196 and 198).

ILLUSTRATION: Figures 28, 29, 52 (skulls, mandibles, and dentition), 30 (limbs).

DISCUSSION

The new genus *Dayohyus* embraces two comparatively low and broad-skulled species. In this respect they differ from all other John Day oreodonts.

Superficially, the skulls appear somewhat similar to the examples of *Promesoreodon scanloni* from "Zone D" of the Brule in the Great Plains but differ in having lighter teeth, a shallower lacrimal fossa, and a heavier and more expanded postglenoid process. The resemblance between *Dayohyus* and *Promesoreodon* of the Promerycochoerinae appears to be just another case of parallelism. *Dayohyus* shows much closer affinities to *Eporeodon* and, hence, is included in the same subfamily with the latter genus.

DISTRIBUTION

Two species of *Dayohyus* are known from lower Miocene (middle and upper John Day = Harrison in part) of Oregon. (See geologic distribution chart, p. 22.)

The assumed phylogenetic sequence of *Dayohyus* is as follows: *D. trigonocephalus* from the middle John Day and *D. wortmani* from the upper John Day.

Summary of Species and Types

Two species of *Dayohyus* from one lower Miocene locality are here recorded:

1. *Dayohyus trigonocephalus* (Cope), from John Day Valley, Oregon. (?Middle John Day = approximate Harrison equivalent.)

Holotype: Skull, A.M. 7505. Figures 28, 29.

2. *Dayohyus wortmani,* new species, from John Day Valley, Oregon. (?Upper John Day = approximate Harrison equivalent.)

Holotype: Skull, U.C. 1911. Figures 28, 29, 52.

1. **Dayohyus trigonocephalus** (Cope)

From questionable middle John Day deposits (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

Eucrotaphus trigonocephalus Cope, 1884a, p. 514.

Eporeodon trigonocephalus (Cope): Roger, 1896, p. 213. Thorpe, 1937, p. 96, pl. 8, figs. 4–6.

Characters

Skull: Average size smaller than examples of *E. occidentalis,* smaller than those of *D. wortmani;* sagittal crest similar to those of *E. occidentalis;* supraoccipital foramen with prominent anterior groove extending forward and downward on side of face; nasal lighter than in examples of *E. occidentalis* (nasal of holotype does not extend posteriorly to anterior border of orbit); premaxilla with sharp rise to nasal, more pronounced than in examples of *D. wortmani;* paroccipital process wide at base, tapering to subround at inferior portion, widest area parallel to anteroposterior axis of skull; auditory bulla oblong anteroposteriorly, with less conical outline than in examples of *E. occidentalis;* hyoidal pit very prominent; posterior palate extending from slight to noticeable distance posterior to M^3.

Mandible: (See generic characters).

Dentition: External styles of molars less prominent than in examples of *D. wortmani.* (See generic characters.)

Limbs: (Unknown).

Measurements: Table 8 (p. 196).

Illustrations: Figures 28, 29, 52.

Discussion

The holotype, A.M. 7505, is an almost perfect skull. The occipital condyles have been restored, but we believe that they probably were more robust than is shown in the restoration.

The type specimen represents a very old individual with P^4 the only completely preserved tooth, and it is worn down almost to the roots. The additional dental characters supplied under the discussion of the genus and species are based on the skull, A.M. 7672, referred to *D. trigonocephalus.*

Cope[1] presented a thorough description of the holotype of *D. trigonocephalus* based entirely on the holotype. As a result, many of his specific characters are not valid, because he did not take into account the individual variation one might expect within a species. As for other John Day oreodonts, Cope made comparisons with *Eucrotaphus jacksoni* and *"E." major.* As discussed on page 165, the holotype of *E. jacksoni* is a posterior portion of a skull and not complete enough for identification.

Thorpe[2] more or less followed Cope's conclusions. He considered, however, that several skulls were referable to this species and wrote: "In the Marsh Collection this species is represented by a comparatively few skulls, all from either Turtle Cove or Bridge Creek. These specimens differ, however, from the type in certain aspects, though not sufficiently to invalidate the identification." Thorpe did not specify what the differences were nor cite the material by number. The present writers believe that the greatest differences between examples of *E. occidentalis* and those of *D. trigonocephalus* are that the latter have comparatively small lacrimal fossae and lack the protuberances on the frontals as compared with the former. On this basis, two specimens of the Yale collection (Y.P.M.) referred to *E. occidentalis* by Thorpe are here considered to be *D. trigonocephalus.*

It should be pointed out that Thorpe also considered that the holotype of *Dayohyus*

[1] 1884a, p. 514.

[2] 1937, pp. 96, 97.

trigonocephalus was collected from the "upper John Day" because of the "light grey matrix" adhering to the skull. It should further be mentioned that the referred examples of this species show evidence of green matrix. The present writers do not believe that the color of matrix is diagnostic (see discussion, p. 199).

Nine specimens are here recorded:

HOLOTYPE

Skull with I^1–P^1 rt. and P^2–M^3 (alv.) (P^3 and M^1 alv.). (w‡‡)	A.M. 7505	From ?middle John Day, North Fork of John Day River, Oregon; collected by C. H. Sternberg, 1879 Figured by Thorpe, 1937, pl. 8, figs. 4–6 This report, figures 28, 29

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM BRIDGE CREEK (COLLECTED BY L. S. DAVIS, 1874):

SKULL — Y.P.M.

Partial skull with P^1–P^2 rt. and P^3–M^3 . . . . (w) 12316

The above specimen was considered to be *Eporeodon occidentalis* by Thorpe (1937, p. 83).

FROM TURTLE COVE:

2 SKULLS AND MANDIBLES

Skull with I^1(alv.)–M^3 (I^2 rt.) and mandible attached with I_1–M_3 . . . . (w+) 12345

The above specimen was considered to be a pleisotype of *E. occidentalis* by Thorpe (1937, p. 83).

Partial skull and mandible (not prepared) . . . . U.O. 672

The above specimen was collected by Thomas Condon.

SKULL — A.M.

Crushed skull with I^1–M^3. Figure 29, 52 . . . . (M+) 7693

The above specimen was collected by J. L. Wortman, 1879.

FROM GENERAL AREA:

4 SKULLS

Partial skull with I^2–P^1 rt. and P^2–M^3(br.) . . . . (w‡) 7568

Anterior portion of skull with C/–P^2 rt. and dP^2–M^3(germ.) . . . . (I) 7579

Partial skull with C/(rt.)–M^3 . . . . (w‡) U.O. 675

The above specimens were collected by Thomas Condon.

1. **Dayohyus wortmani**,[1] new species

From questionably upper John Day (approximately equal in age to the Harrison of the Great Plains), John Day Valley, Oregon

CHARACTERS

SKULL: Larger than in examples of *D. trigonocephalus;* supraorbital foramen with anterior groove, not so prominent or extending down side of face so far as in *D. trigonocephalus;* nasals extending posteriorly to a point opposite anterior border of orbits; orbit oblong, higher than wide, posterior process more massive than in examples of *D. trigonocephalus;* lacrimal fossa smaller than in examples of *D. trigonocephalus;* malar deeper than in above species; paroccipital process wide at base, tapering to a more or less round inferior border; bulla roundish but small for size of skull; postglenoid process more robust than in examples of *D. trigonocephalus.*

MANDIBLE: Postsymphysis below anterior border of P_3; inferior border with prominent downward slope posteriorly; ascending ramus with noticeable inward curve to inferior border; condyle moderately light, external border

[1] Named in honor of J. L. Wortman, the collector of many John Day specimens.

higher than internal; noticeable posterior projection of ascending ramus below condyle.

DENTITION: (See generic description).

LIMBS: Lighter than in examples of *Eporeodon* (*Paraeporeodon*).

MEASUREMENTS: Tables 8 and 9 (pp. 196 and 198).

ILLUSTRATIONS: Figures 28–30, 52.

DISCUSSION

The present writers prefer to consider *Dayohyus wortmani* tentatively an upper John Day form and *D. trigonocephalus* as a middle John Day species. These conclusions are based on size, shape, and other diagnostic characters. This sequence suggests a plausible phylogenetic line.

Ten specimens are here recorded:

HOLOTYPE

Skull with I^1(rt.)–M^3 (P^1–P^2 rt.). (w+)	U. C. 1911	From ?upper John Day, U.C. Coll. Loc. No. 898, John Day Valley, Oregon; collected by Davis and Osmont, 1900 Figures 28, 29, 52

TENTATIVELY REFERRED FROM JOHN DAY VALLEY, OREGON

FROM CAMP CREEK, CROOKED RIVER (COLLECTED BY J. L. WORTMAN, 1879):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull (2 sections) with I^3(alv.)–M^3 (P^1 rt.), mandible with /C–P_2 rt. and P_3–M_3, and humerus. Figures 29, 30	(w+)	A.M. 7655

3 SKULLS

Partial skull with I^1–C/ rt. and P^1(br.)–M^3	(w‡)	7525
Partial skull with C/–M^3 rt.	(w+)	7595
Partial skull with I^1–M^3 (I^3 alv.)	(w‡+)	7654

FROM THE "COVE," GRANT COUNTY (COLLECTED BY C. H. STERNBERG, 1878–1879; DAY AND WARFIELD, 1877):

SKULL AND SKELETAL ELEMENTS

Crushed skull with I^1–M^3, radius, partial ulna, and atlas (1879) Included under above number are a radius and partial ulna about the size of those of *Oreodontoides*. Collected by C. H. Sternberg, 1879.	(w‡)	7725

2 SKULLS

Anterior portion of skull with I^1–P^1 rt. and P^2(br.)–M^3 Collected by Day and Warfield, 1877.	(M+)	7549
Posterior portion of skull with M^1(br.)–M^3	(w+)	7865

FROM "GREEN JOHN DAY", EAST OF JOHN DAY RIVER, BETWEEN MCCARTY AND C. V. BATES RANCHES; "NW. OF C.I.T. LOC. 10":

SKULL

Skull with C/(br.)–M^3 (M^1 alv.)	(w‡+)	C.I.T. 507

FROM "NORTH FORK" (CONDON COLLECTION):

SKULL

Partial skull (not prepared at the time of writing)	U.O. F1050

EXPLANATION OF TEXT FIGURES 24–30

FIG. 24. Lateral, dorsal, and ventral views of skulls: *Eporeodon occidentalis* Marsh, holotype (cast), Y.P.M. 10142 (orbit from opposite side, either the cast or type specimen has been damaged in the glenoid surface area since Thorpe's 1921 illustration), from ?middle John Day (= approximate age of Harrison Formation), Oregon. *E. davisi,* new species, holotype, A.M. 7576, from ?upper John Day (= approximate age of Harrison Formation), Oregon.

Inferior dentition and mandibular ramus: *E. davisi* referred, A.M. 7689 (I_1 and /C from opposite side), from ?upper John Day (= approximate age of Harrison), Oregon. ×½.

FIG. 25. Lateral and dorsal views of skull: *Eporeodon* (*Paraeporeodon*) *pacificus* (Cope), holotype, A.M. 7502 (dentition combination of both sides), from ?middle John Day (= approximate age of Harrison), Oregon.

Lateral views of skulls: *E.* (*P.*) *longifrons* (Cope), referred, A.M. 7591, from ?upper John Day (= approximate age of Harrison), Oregon. *E.* (*P.*) *longifrons perbullatus* (Thorpe), referred, A.M. 7497 (I^3 and C/ from opposite side), from John Day (= approximate age of Harrison), Oregon. *E.* (*P.*) *leptacanthus* (Cope), holotype, A.M. 7695 (combination of both sides), from John Day (= approximate age of Harrison), Oregon. ×½. (See fig. 26.)

FIG. 26. Dorsal and ventral (in part) views of skulls (same as fig. 25): *Eporeodon* (*Paraeporeodon*) *longifrons* (Cope), holotype, A.M. 7504 (P^1–P^2 alv. from opposite side), from ?upper John Day (= approximate age of Harrison), Oregon. ×½. (See figs. 25 and 27.)

FIG. 27. Ventral views of skulls (same as fig. 25). Inferior dentition and mandibular rami: *Eporeodon* (*Paraeporeodon*) *longifrons* (Cope), referred, A.M. 7591 (/C and M_3 restored from opposite side), from ?upper John Day (= approximate age of Harrison), Oregon. *E.* (*P.*) *pacificus* (Cope), referred, A.M. 7557, from ?middle John Day (= approximate age of Harrison), John Day Valley, Oregon. *E.* (*P.*) *leptacanthus* (Cope), referred, A.M. 7694 (P_2–P_4 restored from opposite side), from John Day (= approximate age of Harrison), Oregon. *E.* (*P.*) *longifrons perbullatus* (Thorpe), referred, A.M. 7497, from John Day (= approximate age of Harrison), to Harrison Formation, John Day Valley, Oregon. ×½. (See fig. 26.)

FIG. 28. Lateral and dorsal views of skulls: *Dayohyus trigonocephalus* (Cope), holotype, A.M. 7505, from ?middle John Day (= approximate age of Harrison), Oregon. *D. wortmani,* new species, holotype, U.C. 1911 (combination of both sides), from ?upper John Day (= approximate age of Harrison), Oregon. ×½. (See fig. 29.)

FIG. 29. Ventral views of skulls (same as fig. 28): *Dayohyus trigonocephalus* (Cope), referred, A.M. 7693 (combination of both sides), from ?middle John Day (= approximate age of Harrison), Oregon.

Inferior dentition and mandibular rami: *Dayohyus wortmani,* new species, referred, A.M. 7655, from ?upper John Day (= approximate age of Harrison), Oregon. ×½.

FIG. 30. Comparison of skeletal elements: A, *Eporeodon occidentalis* Marsh; B, *E. davisi,* new species; C, *E.* (*Paraeporeodon*) *pacificus* (Cope); D, *E.* (*P.*) *longifrons* (Cope); E, *?E.* (*P.*) *longifrons perbullatus* (Thorpe) (possibly an example of *Epigenetochoerus parvusi,* fig. 22, p. 191); F, *E.* (*P.*) *leptacanthus* (Cope); G, *Dayohyus wortmani,* new species. ×½.

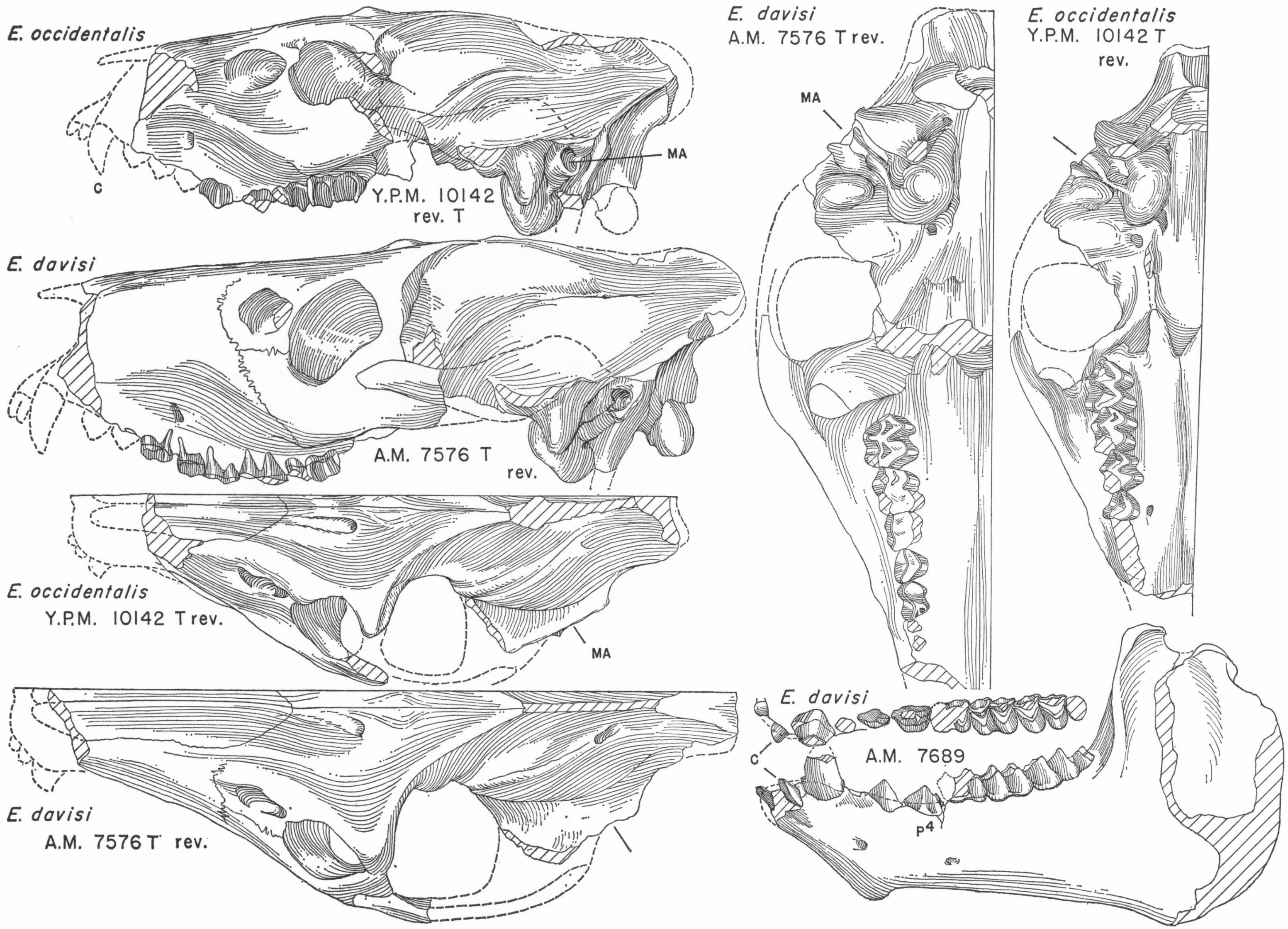


FIG. 24. *Eporeodon,* two species, holotypes, Y.P.M. 10142 (cast) and A.M. 7576, and referred, A.M. 7689. (See p. 219.) ×½.

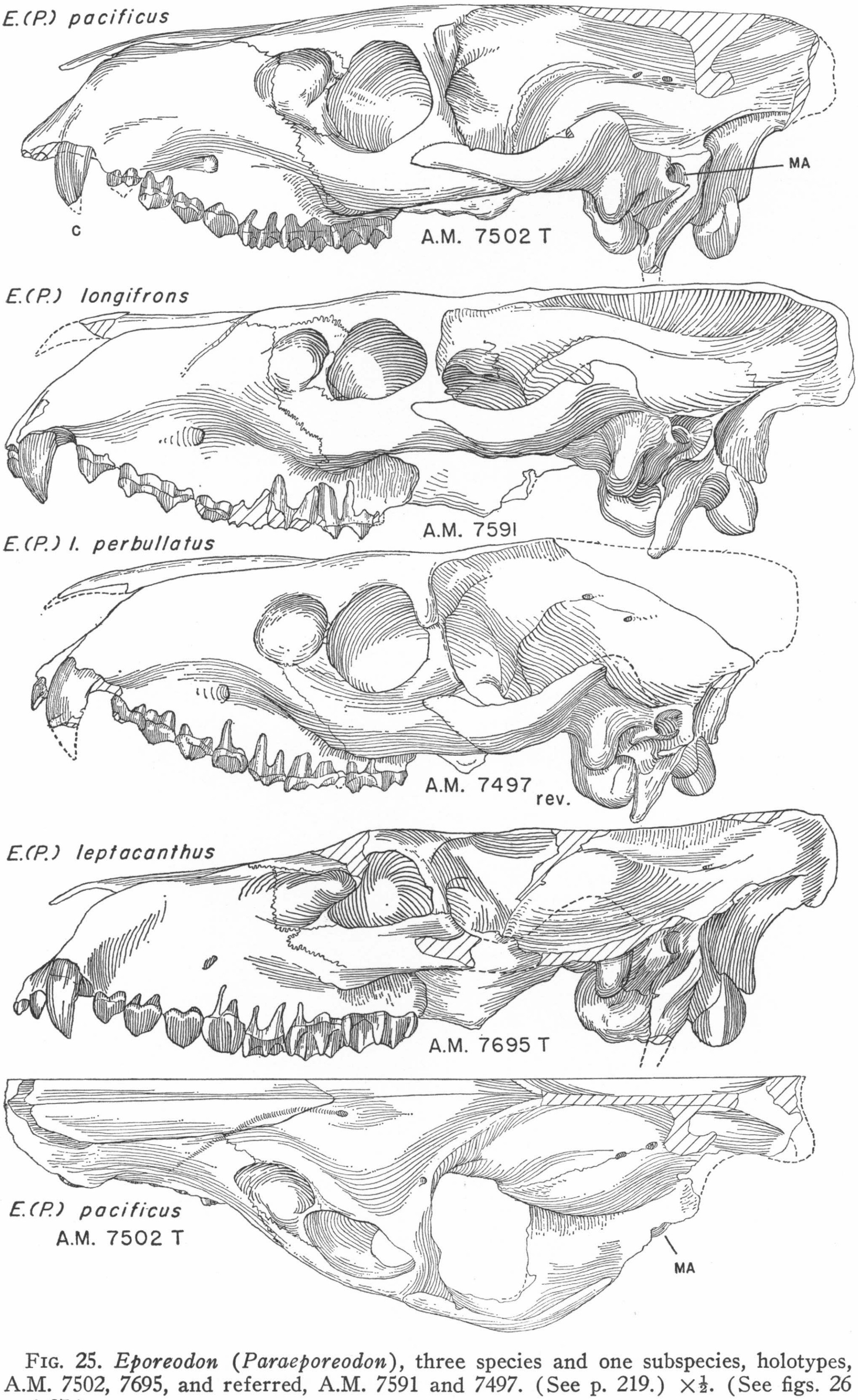


FIG. 25. *Eporeodon* (*Paraeporeodon*), three species and one subspecies, holotypes, A.M. 7502, 7695, and referred, A.M. 7591 and 7497. (See p. 219.) ×½. (See figs. 26 and 27.)

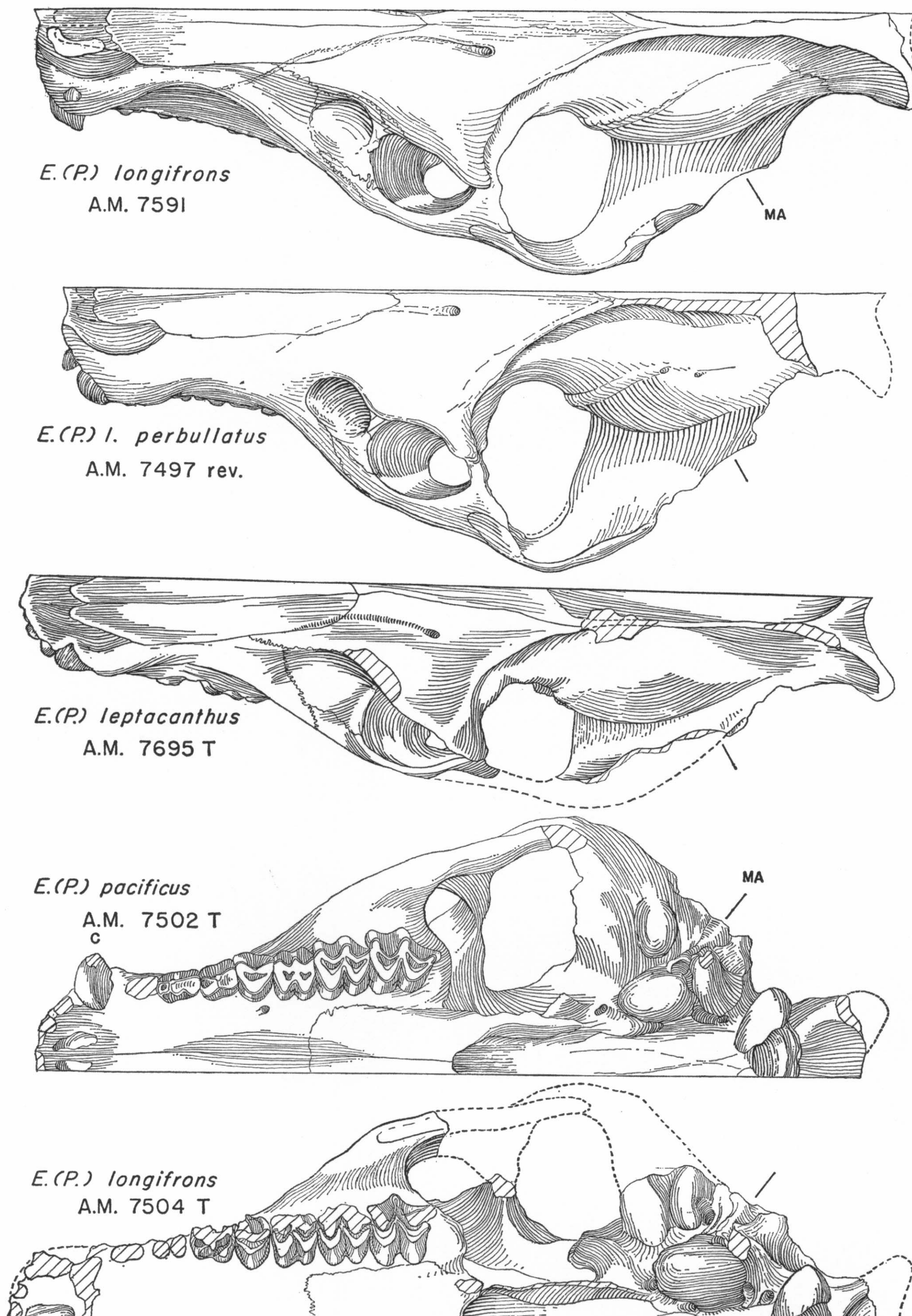


FIG. 26. *Eporeodon* (*Paraeporeodon*), four species, holotypes, A.M. 7695, 7502, 7504, referred, A.M. 7591 and 7497. (See p. 219.) ×½. (See figs. 25 and 27.)

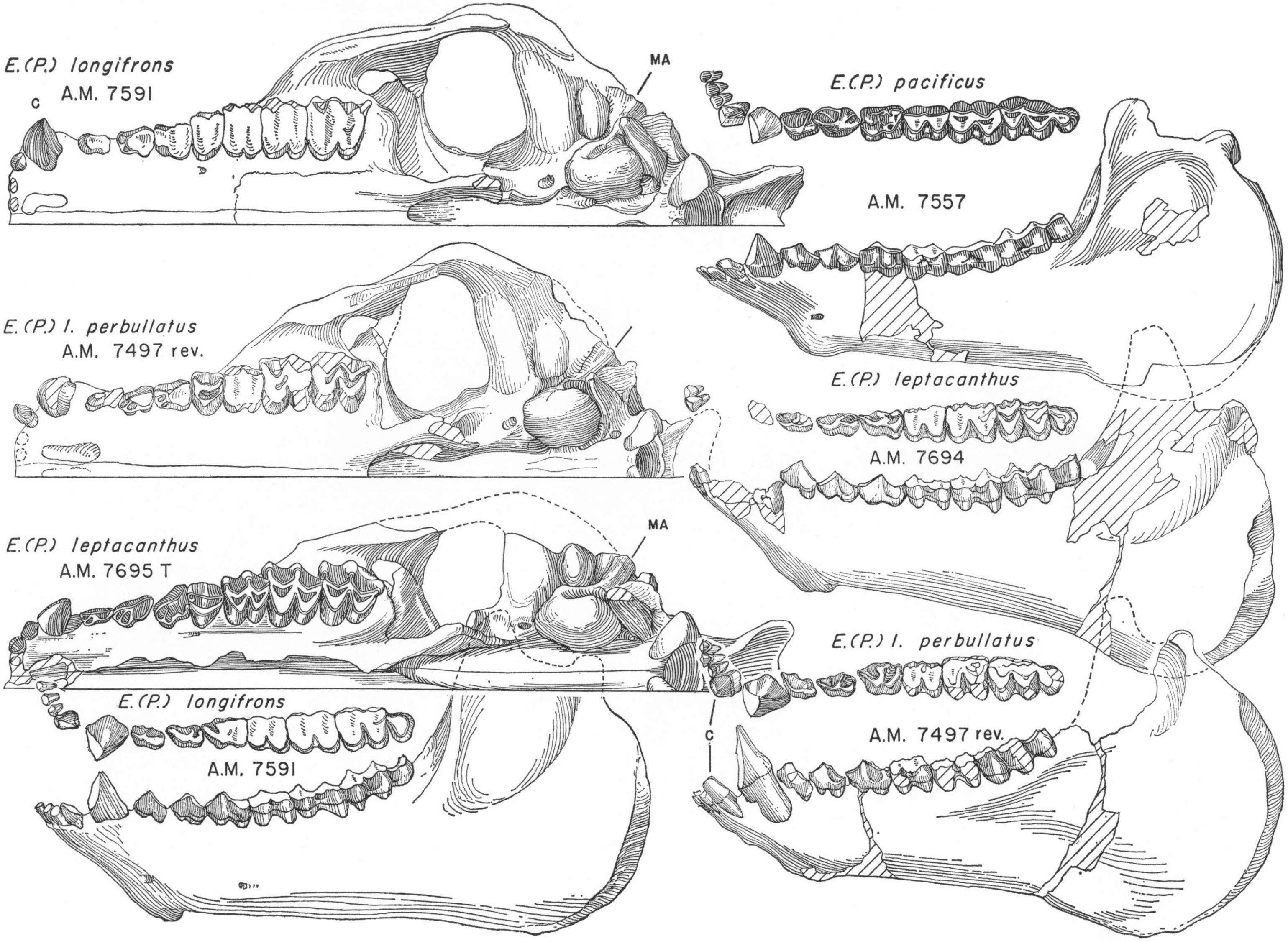


Fig. 27. *Eporedodon* (*Paraeporeodon*), four species, holotype, A.M. 7695, and referred, A.M. 7591, 7497, 7591, 7557, 7694, and 7497. (See p. 219.) $\times\frac{1}{2}$. (See figs. 25 and 26.)

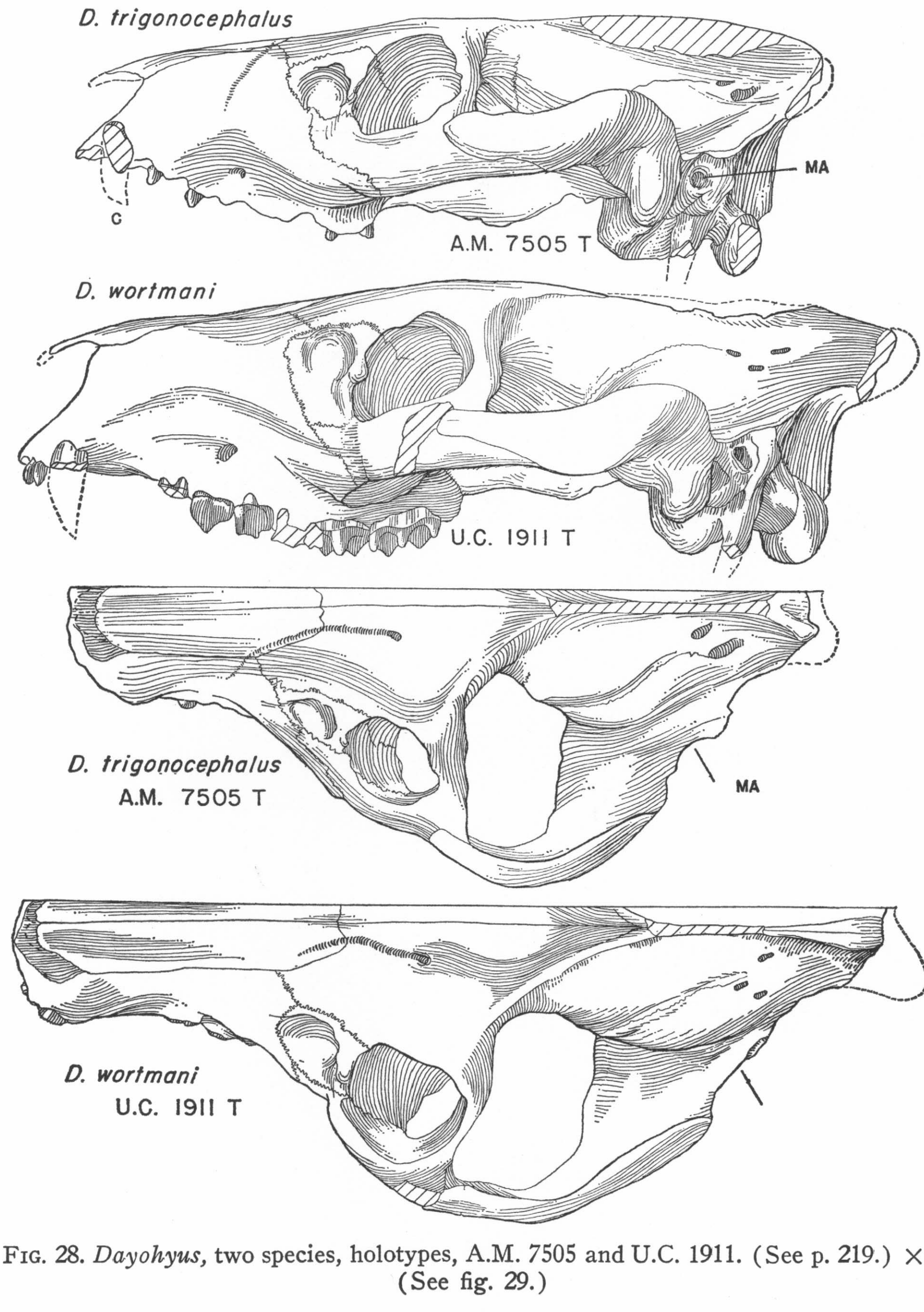


FIG. 28. *Dayohyus,* two species, holotypes, A.M. 7505 and U.C. 1911. (See p. 219.) $\times\frac{1}{2}$. (See fig. 29.)

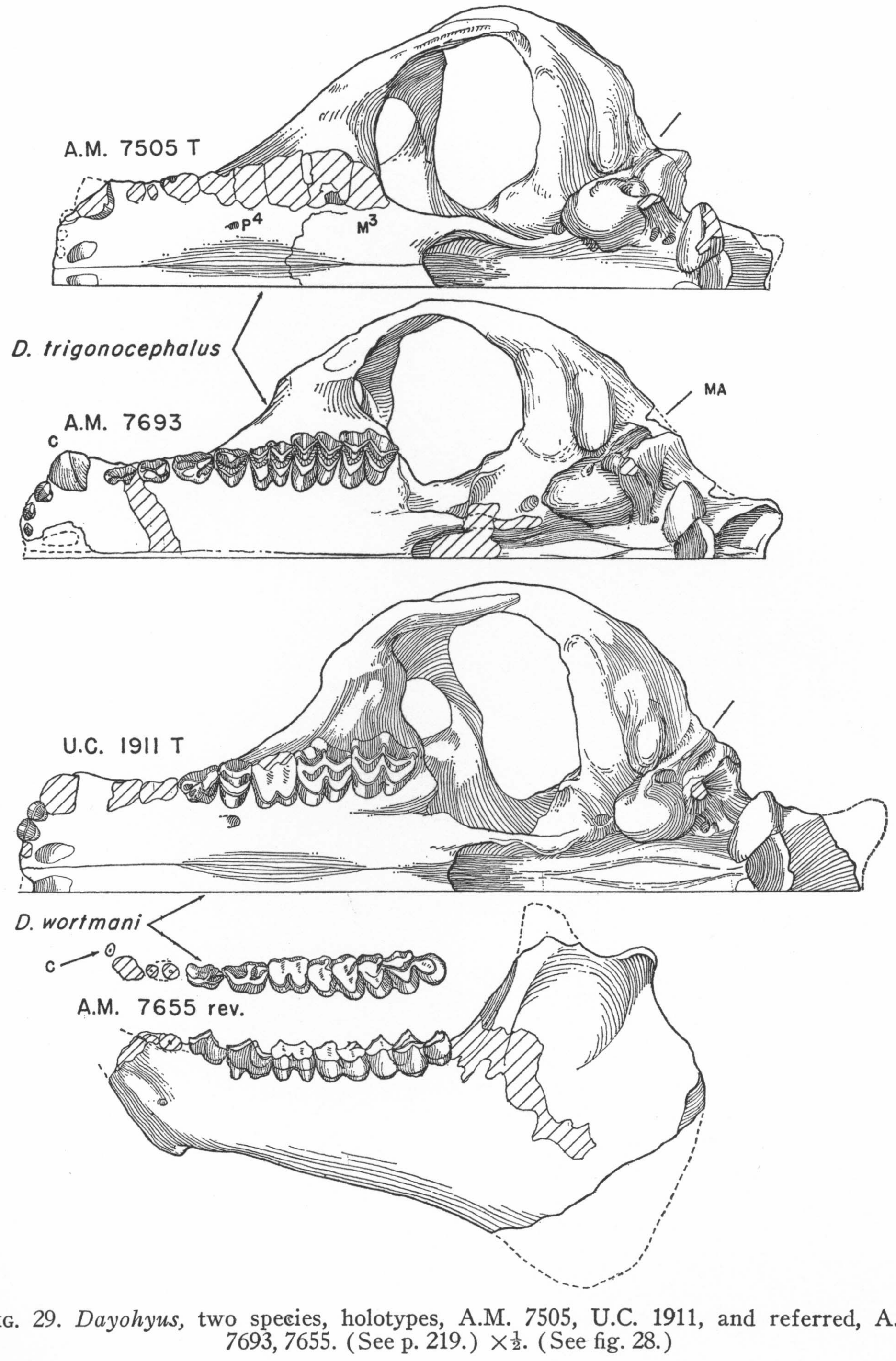


FIG. 29. *Dayohyus,* two species, holotypes, A.M. 7505, U.C. 1911, and referred, A.M. 7693, 7655. (See p. 219.) ×½. (See fig. 28.)

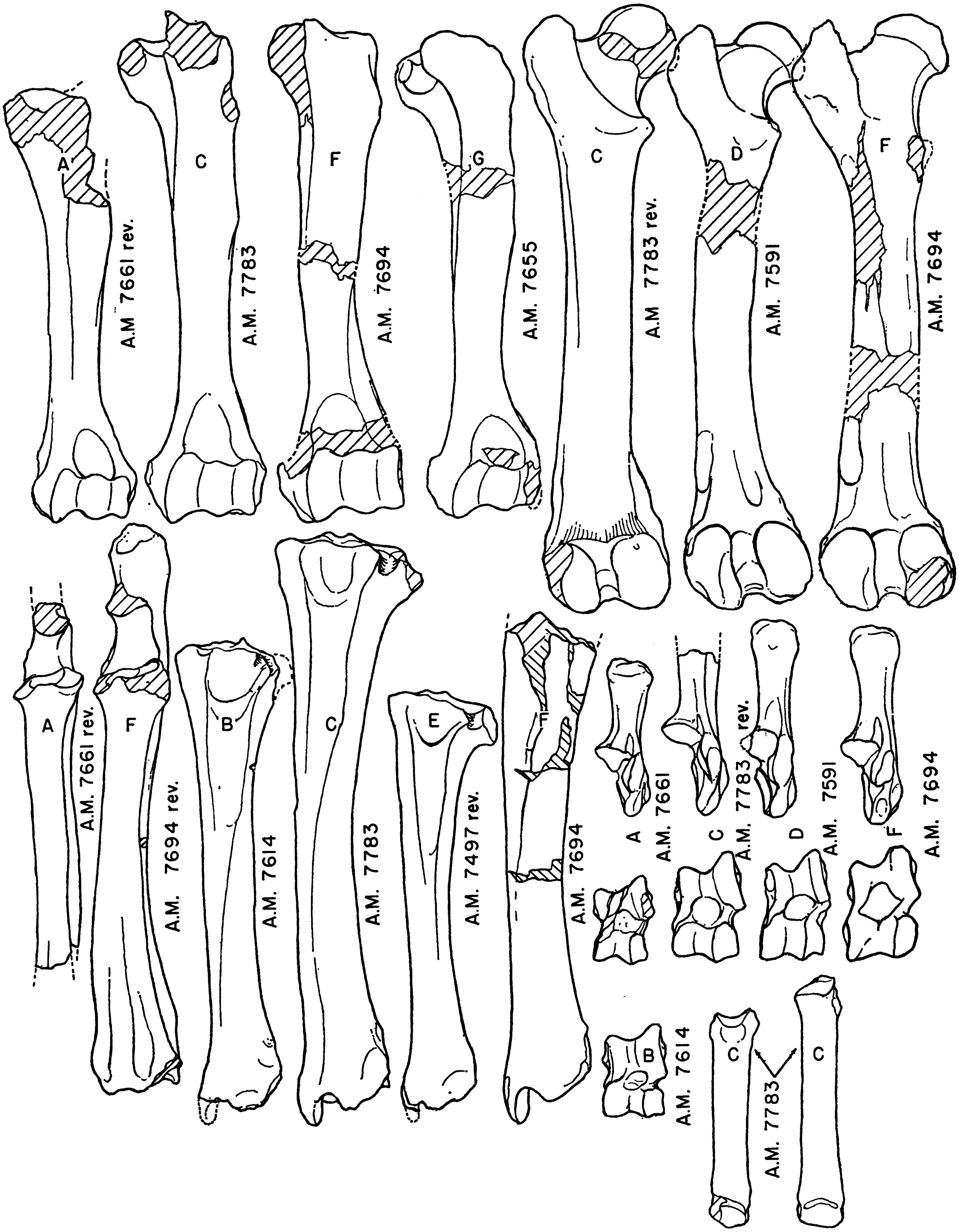


FIG. 30. Comparison of limb elements: A, *Eporeodon occidentalis*; B, *E. davisi*. C, *E.* (*Paraeporeodon*) *pacificus*; D, *E.* (*P.*) *longifrons*; E, *E.* (*P.*) *l. perbullatus*; F, *E.* (*P.*) *leptacanthus*; G, *Dayohyus wortmani*. (See p. 219.) ×½.

DESCRIPTION OF LEPTAUCHENIINAE[1] SCHULTZ AND FALKENBACH, SUBFAMILY 11[2]

THE SUBFAMILY LEPTAUCHENIINAE includes two new tribes, the Sespiini and the Leptauchiniini. (The Sespiini embrace two closely related genera, *Sespia* Stock and *Megasespia*, new genus, and the Leptaucheniini contain five genera, *Pithecistes* Cope, *Leptauchenia* Leidy, *Cyclopidius* Cope, *Hadroleptauchenia*, new genus, and *Pseudocyclopidius*, new genus). Skulls of very small to small size (smallest examples similar in size to smallest known oreodonts, *Bathygenys alpha*, from the Chadron, and largest examples approach size of *Merychyus arenarum* from the lower Marsland deposits); dolichocephalic to brachycephalic; facial region shortened; supraoccipital wings expanded and widely spread, incorporated into a fan-shaped occipital region, slight posterior projection of superior border to region above posterior border of condyles; sagittal crest moderately low to high; brain case rather low, inflated laterally; anterior portion of frontals with varying degree of invasion by nasal-facial vacuity; nasals varying in comparative lengths and widths depending on degree of invasion of nasal-facial vacuity into frontal and maxilla regions, nasals extremely narrow except at anterior border which widens for contact with maxilla; anterior nasal-maxilla contact in area directly above or in front of anterior border of C/; supraorbital foramen small (frequently two occur on each side); orbit small to large in size (larger proportionately in the Sespiini), roundish, directed markedly upward, forward, and outward, orbit differing from that of other oreodonts in possessing an anterior, internal opening (below lacrimal bone) extending into nasal-facial vacuity (see fig. 54, arrow in drawings indicates opening); malar moderately deep to extremely deep below orbit, massive; zygoma greatly reduced; infraorbital foramen in area above posterior portion of P^3; lacrimal fossa minute; lacrimal bone very small (reduction due to invasion of region by nasal-facial vacuity); nasal-facial vacuity[3] very large, bounded by maxilla, nasal, frontal, and lacrimal bones; slight depression of face above premolars, less prominent than in most subfamilies of oreodonts; premaxillae joined; occipital condyles small for size of skull; paroccipital process very wide at base, incorporated into the fan-shaped occipital, tapering noticeably down to a peglike tip; bulla greatly inflated (proportionately smaller in the Sespiini), rounded, crowding paroccipital and postglenoid processes and extending inwardly almost to midline of skull, bulla hollow internally (see fig. 55); external auditory meatus placed high above bulla and at external edge of supraoccipital wing, opening outwardly and posteriorly; postglenoid process narrow anteroposteriorly and comparatively short vertically, crowded by bulla; glenoid surface wide laterally, with noticeable depression or groove extending laterally just anterior to postglenoid process; posterior palatine border from slightly anterior to posterior border of M^3 to just posterior of M^3; mandible light to robust; postsymphysis from below posterior border of P_2 to anterior border of M_1; ramus moderately deep to deep; symphysis with sharp downward slope some examples with marked overhang of incisive border; inferior border of ramus more or less straight to a point below posterior part of M_3, with slight downward slope beyond this point; ascending ramus moderately high to high, long anteroposteriorly; condyle light, external border higher and more posterior than internal border; teeth subhypsodont to extremely hypsodont (in the Sespiini); dental formula, $I\frac{2}{3}$ or $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, and $M\frac{2}{3}$ or $M\frac{3}{3}$; incisors more peg-shaped; external styles of molars from almost absent (from the Sespiini) to prominent (in the Leptaucheniini); superior and inferior molars without anterior or pos-

[1] The term "leptauchenin" is used in the present report as a common name for the subfamily, although earlier the present writers (1956, p. 453) used "leptauchenid" in this sense.

[2] Schultz and Falkenbach, 1940, p. 215. For references to previously described subfamilies, see pages 19 and 491 of the present report.

[3] The term "nasal-facial vacuity" is used to distinguish the area from a facial vacuity which does not invade the nasal bone and little, if any, of the frontal. The nasal-facial vacuity invades the maxilla, nasal, frontal, and lacrimal bones and also opens into the orbit through the usually solid anterior orbital wall.

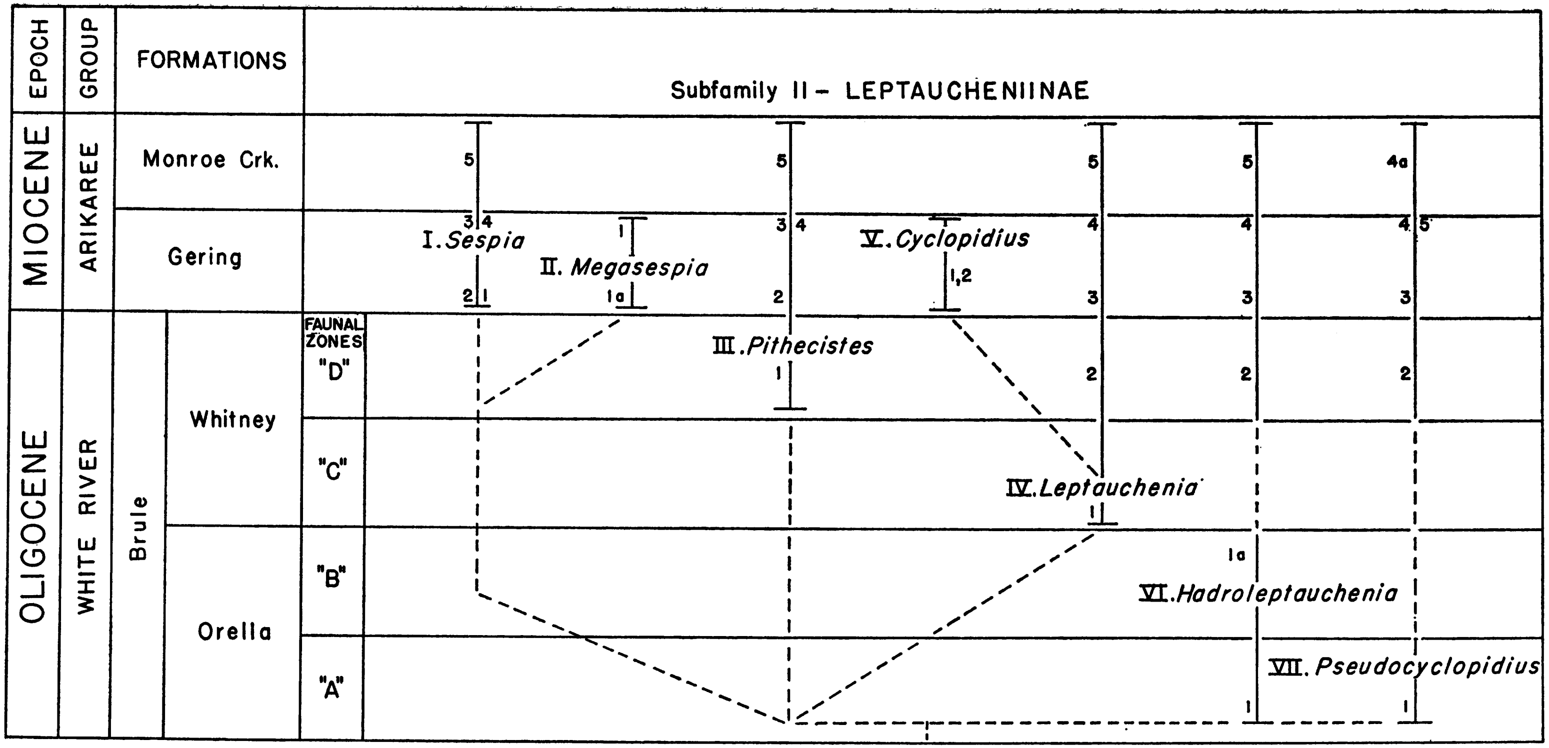


CHART 8. Stratigraphic distribution of the Leptaucheniinae (subfamily 11). See stratigraphic distribution of 10 previously reported subfamilies of oreodonts (Schultz and Falkenbach, 1949, p. 80; 1954, p. 156; 1956, p. 382; present paper, pp. 24, 193, 227).

EXPLANATION OF CHART 8. The continued use of faunal zones[1] in this report is necessary to indicate approximate age equivalents of Oligocene deposits in the various areas in the Great Plains until more definite geologic correlations are established.

The known geologic range of each genus and subgenus is indicated by a solid vertical line, with a horizontal bar at each end. Where relationship between two phyla is questioned, the line is broken.

The numbers used here for species and subspecies are the same as those in the table of contents of this report. The numbers to the left of a vertical line indicate forms from the west-central Great Plains region (Nebraska, South Dakota, and Wyoming); those to the right, from localities outside this area (California and Montana).

Subfamily 11. Leptaucheniinae
- A. Sespiini, new tribe
  - I. *Sespia* Stock
    - 1. *S. californica* (Stock)
    - 2. *S. marianae*, new species
    - 3. *S. nitida* (Leidy)
    - 4. *S. heterodon* (Cope)
    - 5. *S. ultima*, new species
  - II. *Megasespia*, new genus
    - 1. *M. middleswarti*, new species
    - 1a. *M. middleswarti*, geologic variety
- B. Leptaucheniini, new tribe
  - III. *Pithecistes* Cope
    - 1. *P. tanneri*, new species
    - 2. *P. mariae*, new species
    - 3. *P. altageringensis*, new species
    - 4. *P. brevifacies* (Cope)
    - 5. *P. copei*, new species
  - IV. *Leptauchenia* Leidy
    - 1. *L. harveyi*, new species
    - 2. *L. decora* (Leidy)
    - 3. *L. martini*, new species
    - 4. *L. parasimus*, new species
    - 5. *L. margeryae*, new species
  - V. *Cyclopidius* Cope
    - 1. *C. simus* Cope
    - 2. *C. emydinus* Cope
  - VI. *Hadroleptauchenia*, new genus
    - 1. *H. eiseleyi*, new species
    - 1a. *H. eiseleyi*, geologic variety
    - 2. *H. primitiva*, new species
    - 3. *H. shanafeltae*, new species
    - 4. *H. densa* (Loomis)
    - 5. *H. extrema*, new species
  - VII. *Pseudocyclopidius*, new genus
    - 1. *P. orellaensis*, new species
    - 2. *P. frankforteri*, new species
    - 3. *P. major* (Leidy)
    - 4. *P. lullianus* (Thorpe)
    - 4a. *P. lullianus expiratus*, new geologic subspecies
    - 5. *P. quadratus* (Koerner)

[1] Falkenbach and Schultz, 1951, p. 47; Schultz and Falkenbach, 1954, p. 153; 1956, p. 382; the present paper, p. 411.

terior intermediate crests; enamel thin on crowns of teeth, tooth patterns obliterated with small amount of wear[1]; limbs small in size, largest examples approaching those of *Miniochoerus* (*Paraminiochoerus*) *gracilis* (Leidy), Schultz and Falkenbach[2]; comparatively heavy for their length.

Discussion

The Leptaucheniinae have been the basis for much discussion because of the unique nasal-facial vacuities and the elevated position on the depressed skull of the nasal, orbit, and external auditory meatus. The possibility that the leptauchenins were "water-living" forms was first advocated by Cope,[3] who wrote: "The concavity of the superior border of the premaxillary bones [of *Leptauchenia* (*Cyclopidius*)], together with their upward production, leads me to suspect that the external nares were superior in position. This is the indication of an aquatic habit of life, such as is led by the hippopotamus. Like that animal, the nostrils of *Cyclopidius* were probably valvular to prevent the ingress of the water. The animals probably passed much of their time in the water, and the nostrils could be brought to the surface for the purpose of respiration, while the remainder of the head and body remained concealed. The prominent rim of the auditory meatus suggests a similar valvular closure of the organ of hearing and is also a provision for its easy approximation to the surface of the water when necessary."

The theory of an aquatic habitat has also been supported by many other paleontologists, including Matthew[4] and Scott.[5] Scott wrote that "the position of the nostrils, orbits, and auditory tubes is like that of a miniature hippopotamus and strongly suggests aquatic habits."

Later Scott,[6] in a discussion of the habits of *Leptauchenia*, was even firmer in his belief that leptauchenins were "habitually" aquatic animals. He challenged both Sinclair's[7] and Thorpe's[8] contentions that the leptauchenins were not aquatic forms. Sinclair had suggested that the feet of *Leptauchenia* were well adapted for walking and running on firm ground. Scott,[9] however, wrote: "No terrestrial ungulate has such tiny hoofs, which are more claw-like than hoof-like in shape, and they are entirely different from those of others of the family. The manus of *Cyclopidius* [*Hadroleptauchenia*], as figured by Loomis, is actually suggestive of webbed feet; for terrestrial locomotion it would appear to be well-nigh useless." Thorpe[10] had reported that the osteological characters did not support the aquatic habits of *Leptauchenia*, and he concluded: "Coupled with these factors [morphological evidence] is the lack of their remains in river deposits [*Protoceras* channels, etc.], as mentioned above, and this combination apparently casts grave doubt on the inference that any of the oreodonts were aquatic or amphibious."

The present writers believe that the leptauchenins, at least the species attributed to the tribe Leptaucheniini, definitely were not aquatic or amphibious forms. Paleoecological as well as osteological evidence indicates that these animals lived in extremely arid areas during late Oligocene times, away from the valleys and streams, and perhaps it was not necessary for them even to drink water. They could have absorbed sufficient moisture from the desert type of vegetation that they must have consumed. The writers have examined the skulls of various desert antelopes from Africa and Asia, and have found that the skulls have certain characters in common with those of the leptauchenins, including large tympanic bullae, facial vacuities, and specialized nasal areas. The skulls of the addax (*Addax nasomaculatus*), the gemsbok (*Oryx gazella*), the leucoryx (*Antilope leucoryx*), the addra gazelle (*Gazella dama ruficollis*), the dorcas gazelle (*Gazella dorcas*), the scimitar oryx (*Aegoryx algazel*), and other antelopes were observed. It is interesting to note that some of the desert antelopes, such as the gemsbok, are "perfectly

[1] The thin enamel on the crowns of the teeth is similar to that found in the Miniochoerinae (Schultz and Falkenbach, 1956, p. 391). The molar fossettes are shallow, and the coatings of enamel are thin on the crowns. The enamel was lost along with crown patterns after a short period of wear on the teeth.

[2] 1956, p. 413.

[3] 1884a, p. 547.

[4] 1899a, p. 404; 1899b, p. 24.

[5] 1937.

[6] 1940, p. 707.

[7] 1910, p. 198.

[8] 1937, p. 24.

[9] 1940, 709.

[10] 1937, p. 24.

independent of water," and rarely, if ever, drink it.[1] The skulls of other desert mammals such as the gerboa, the kangaroo rat, and the desert fox were also examined for further clues which might aid in the interpretation of the leptauchenin skulls. The habits of all these forms were studied from the literature. The Leptaucheniini of the late Oligocene (oreodont faunal "Zone D," see charts 13, 15) are considered to be desert forms for the following reasons:

1. These oreodonts lived in divide or upland areas, which apparently were very arid (see discussion of paleoecological conditions of the late Oligocene, p. 407).

2. No specimens of the Leptaucheniini have been reported from *Protoceras* channels or other channels in the Middle or Upper Whitney deposits ("*Leptauchenia* beds"). Also no leptauchenins have been recorded from channels or valley phase of the Lower Whitney sediments ("Upper *Oreodon* beds"). Undoubtedly some bones of leptauchenins were washed down the slopes to the stream areas during heavy rain storms, and thus remains of these oreodonts may be found in the channel or flood-plain deposits.

3. The various species of the Leptaucheniini all have unusually small orbits, in contrast to those of other oreodonts that lived during the Oligocene. Small orbits are ideal for protection of the eyes from dust, ash, and fine sand.

4. The large tympanic bullae of the Leptaucheniini suggest that the animals had a good sense of hearing. Large bullae are frequently associated with mammals that live in the deserts today. Good hearing affords protection to the animals in open country during dust or sand storms. Leptauchenins probably had large external ears situated at the rear of the skull which would aid in hearing. Many animals living today in open or upland regions have ears of this type.

Douglas B. Webster,[2] in reporting on a function of the enlarged middle-ear cavities of the kangaroo rat, *Dipodomys*, reached some interesting conclusions, which may aid in the interpretation of the enlarged bullae of the leptauchenins. Webster summarized his work as follows:

"1. Inasmuch as a 75 per cent bilateral reduction of the volume of the kangaroo rat's middle-ear cavity has no discernible affects on the animal's locomotion, it is concluded that the hypertrophied mastoid bullae are not concerned with vestibular functions.

"2. Cochlear microphonics are largest between 1,000 and 3,000 cps with peaks of extraordinary sensitivity at 1,200 or 1,400 cps, 1,800-2,200 cps, and 2,600 cps.

"3. Experimental reduction of the middle-ear volume reduces the cochlear microphonics especially between 1,000 and 3,000 cps, although the most sensitive peaks remain discernible. Removal of the dorsal walls of the mastoid bullae have little effect on the microphonic response.

"4. Experiments with owls and rattlesnakes indicate that unoperated kangaroo rats can avoid predation but that operated animals with reduced middle ear volumes cannot. Sonagrams of sounds produced during an owl's flight and a rattlesnake's strike contain frequencies which come within the kangaroo rat's most acute hearing range.

"5. It is concluded that the kangaroo rat's hypertrophied mastoid bullae reduce the damping of the tympanoossicular system sufficiently to allow resonance phenomena to occur, thus increasing the ear's sensitivity for the resonant frequencies. This increased auditory sensitivity enables the kangaroo rat to detect predators."

5. The specialized nasal bones and the associated vacuities indicate that these animals had some sort of breathing tubes, similar to some found in desert antelopes today. It seems reasonable to suspect that the vacuity housed a "sponge" or tubular arrangement that screened out the dust from the air as it entered the nasal. Also the fact that the vacuity opened directly into the orbit (see fig. 54) may suggest that the tear (lacrimal) duct supplied moisture to the "sponge" area, which may have aided in the elimination of the accumulated dust.

6. The skulls of all the upper Oligocene Leptaucheniini are low, flat, and broad, with the nasal opening, orbit, and the external auditory meatus all situated on the top of the skull. This "streamlining" could indicate an adaptation in order to face the strong dusty winds. In the various leptauchenin phyla it is apparent that in the sequence development

[1] Sclater and Thomas, 1894-1900 (1899, vol. 4), p. 57.

[2] 1962, p. 248; see also 1961, p. 123.

(geologically) the nasal-facial vacuity invaded more posteriorly into the frontal and reduced the size of the lacrimal bone. A small nasal septum seems to be present, but there is no evidence of turbinates. The nasal-facial vacuity is unusual in that it extends posteriorly under the lacrimal bone and into the orbit. This situation differs from the condition in all other oreodonts, in which the nasal passage and the orbit are separated by a solid wall of bone.

7. The postcranial skeleton is readily comparable with that of other oreodonts. The slender toes (five in the front and four in the hind feet), as well as the limb elements, seem well adapted for running and living in dry dusty areas. The feet of the hyracodonts, which lived contemporaneously with the late Oligocene leptauchenins, are even more specialized for a cursorial life. In this group the limbs are long and slim, with but three toes on the hind as well as the front feet.

Sinclair[1] stated, ". . . in a general way, there is a good deal of resemblance between the writer's restoration of *Leptauchenia* (Fig. 1) and Peterson's reconstruction of *Phenacocoelus*." Sinclair's statement was perhaps influenced by Peterson's earlier report.[2] Schultz and Falkenbach[3] have previously reported the following in their revision of the genus *Phenacocoelus:* "Peterson in the original description of *Phenacocoelus* stated: 'The genus belongs to the family Agriochoeridae, revealing affinities to *Leptauchenia* or *Cyclopidius.*'

"This conclusion was based, perhaps, on the presence of the frontal vacuities in *Phenacocoelus typus* and the large [nasal-] facial vacuities of *Leptauchenia* and *Cyclopidius* as well as the large inflated bullae of all three genera."

Sinclair further stated that the claim that *Leptauchenia* was aquatic "is not altogether substantiated by the feet, the slender toes of which terminate in small hoof-like elements well adapted apparently, so far as their structure is concerned, to running on firm ground."

Loomis[4] considered that "the skeleton [of *Leptauchenia*] is lightly built and slender, somewhat like *Merychyus,* except that there are five toes on the front foot." This character was also discussed by Thorpe.[5] The present writers do not consider the occurrence of the five-toed forefoot as a generic or subfamily character. Some examples possessed five toes, but others had only four. There apparently was a tendency among the Miocene leptauchenins to lose metacarpal I. One skeleton of *Pseudocyclopidius lullianus* in the Frick Collection, F:A.M. 57090, from the upper Gering has a fifth digit preserved on the manus. This is the only known species of a Miocene leptauchenin which retained the fifth digit. Undoubtedly, when more skeletons of *P. major* from the lower Gering have been found, there also will be evidence of the fifth digit, although the mounted skeleton U.N.S.M. 1081 shows no evidence of this element. (See Schultz and Falkenbach's discussion of the pollex.[6])

Thorpe[7] also interpreted Loomis'[8] phylogeny chart and reported, "Loomis thinks that these two lines, *Merychyus* and *Leptauchenia,* branched off from the same stock in the lower Oligocene, perhaps from the light-limbed *Limnenetes* line." Loomis',[9] Schlaikjer's,[10] and Thorpe's[11] phylogenies of the oreodonts in general differ considerably from the phylogeny of the present authors see (p. 416). Loomis considered *Limnenetes* the ancestral stock for *Merychyus*[12] and questionably also for *Leptauchenia.*

Schlaikjer accepted the phylogeny suggested by Loomis but was more explicit concerning the specific geologic distribution of the various genera. Schlaikjer proposed that *"Limnentes"* [*Limnenetes*] questionably gave rise to *Leptauchenia* which in turn was the ancestral stock of *Cyclopidius* and stated, "Of the scanty remains described from the early Oligocene deposits, *Limnentes* Douglass seems, as regarded by

[1] 1910, p. 196, fig. 1.
[2] 1906, p. 30.
[3] 1950, p. 104.
[4] 1924b, p. 14.

[5] 1937, p. 235.
[6] 1956, p. 384.
[7] 1937, p. 235.
[8] 1924, fig. 8, p. 15.
[9] 1924b, fig. 8, p. 15.
[10] 1935, fig. 11, p. 168.
[11] 1937, fig. 2, p. 25.
[12] Schultz and Falkenbach, 1949, chart 1, p. 80. There is a considerable period of time between the last occurrence of *Limnenetes* in the early Oligocene (middle Chadron) and the first occurrence of *Merychyus* in the latter part of the early Miocene (Harrison). The forms are comparable in size, but show no evidence of being related.

Loomis . . . to be the most likely ancestor [for *Leptauchenia*] although, when more completely known, it may be found to be nearer the *Eporeodon* line." In figure 11, Schlaikjer also considered *"Leptauchenia nitida"* as the ancestor of all the leptauchenins, presumably because of the size of the skull of *Sespia nitida* and the mistaken identification of the deposits from which the latter type was secured. The deposits from which the remains of *L. nitida* were obtained are actually lower Miocene and not Oligocene (see p. 247).

Schultz and Falkenbach[1] discussed the possibilities of the relationship of the leptauchenins and stated: ". . . the present writers fail to see any direct connection between the two forms [*Limnenetes* and *Leptauchenia*]. It seems reasonable to suspect that the ancestors of the leptauchenids would have possessed some indications of facial vacuities, but *Limnenetes* does not exhibit this character." The writers now believe, however, that *Oreonetes,* or perhaps *Limnenetes,* may have given rise to the leptauchenins. This reversal of opinion is due to the fact that leptauchenin examples are known for the first time from oreodont faunal zones "A," "B," and "C." Additional specimens, especially from "Zone C" of the Chadron, will undoubtedly aid in a solution of the true phylogenetic relationships between the two subfamilies Oreonetinae and Leptaucheniinae.

Both Loomis and Thorpe independently presented phylogenetic charts lacking specific geologic designations for the various phylogenetic lines. Loomis considered *Oreonetes* the ancestral line of *Merycoidodon* and *Limnenetes* as questionably ancestral to *Leptauchenia.* Thorpe differed from Loomis in supposing that *Oreonetes* gave rise to *Limnenetes* which in turn was ancestral to *Leptauchenia* and *Cyclopidius.*

All three of the above-mentioned phylogeny charts either question or show the relationships with broken lines. The present writers' phylogenetic interpretation is considerably different from all previous presentations; this is to be expected when the phylogeny is based on the geologic occurrences of all specimens. (See charts 8, 15, and 16.)

Scott's[2] conclusions with respect to both Loomis' and Thorpe's phylogeny charts were reported under "LIMNENETES-LEPTAUCHENIA-CYCLOPIDIUS Tribe." These conclusions are discussed under the Leptaucheniini.

A worthwhile description with conclusions on the dentition of the leptauchenins was published by Loomis,[3] who stated: "The premolars of the *Leptauchenia* seldom show their pattern, since they are hypsodont and almost always badly worn. When, however, little-worn teeth are studied, it is seen that the upper premolars are shortened by the almost complete suppression of the anterior basin." This is relative to the thin enamel on the crowns of the teeth, which is lost with slight wear. (See discussion, p. 230.)

Schlaikjer[4] made the following observations concerning the leptauchenins: "A study of the skulls in particular of the *Leptauchenia-Cyclopidius* group of oreodonts reveals a number of important facts of which the following are the outstanding:

"1. The molar teeth are sphenoidal in general form,—that is, the anteroposterior dimension is greater near the base of the crown. [This is true except that M^3 becomes longer anteroposteriorly with wear, as was pointed out in *Merychyus*[5] and occurs in all oreodonts. The molars (except M^3) become shorter anteroposteriorly and wider transversely. The latter is extremely noticeable in most Oligocene oreodonts.]

"2. With wear, therefore, the molar teeth [except M^3] become shorter and broader. [It should also be noted that the dentitions of the leptauchenins lost the enamel on the crowns with slight wear (see discussion, p. 230).]

"3. There is considerable variation in the premolar teeth, especially in P^3. [The premolars do show considerable variation (the molars vary in the degree of hypsodonty).] . . .

"5. It appears that with age the skull becomes more brachycephalic. [There seems to be a lack of confirmation of this character in the material available to the present authors. However, there is a tendency in the Leptaucheniini for the skulls to become more brachycephalic in the lower Miocene, but not owing to an indi-

[1] 1956, p. 453.
[2] 1940, p. 687.
[3] 1924, p. 14.
[4] 1935, p. 168.
[5] Schultz and Falkenbach, 1947, fig. 12.

DISTINCTIVE CHARACTERS OF THE LEPTAUCHENIINAE[1]

	Skull	Basal Lengths of Skulls	Sagittal Crest	Frontals[2]	Posterior Margin of Facial Vacuity	Molars	External Styles on Superior Molars
SESPIINI							
I. *Sespia* (p. 239, figs. 31, 38–43, 53)	Extremely small	72–83 mm.	Moderately low and light with slight downward slope posteriorly	Extremely narrow between orbits, unreduced anteroposteriorly	Opposite anterior portion of orbit	Extremely hypsodont, compressed laterally	Weak to absent
II. *Megasespia* (p. 254, figs. 31, 38, 40, 43, 53)	Moderately small	(92) mm.	Higher than in *Sespia*, slight downward slope posteriorly	Moderately narrow between orbits, unreduced anteroposteriorly	Opposite anterior portion of orbit	Extremely hypsodont, compressed laterally	Weak to absent
LEPTAUCHENIINI							
III. *Pithecistes* (p. 258, figs. 32, 38, 40, 53)	Approximately same size as in *Megasespia*	(89)–96 mm.	Higher than in *Sespia*, slight downward slope posteriorly	Narrow between orbits, reduced anteroposteriorly	Opposite anterior border to medial border of orbit	Subhypsodont to hypsodont, expanded laterally more than in *Sespia*	Prominent
IV. *Leptauchenia* (p. 272, figs. 33, 38, 40, 41, 43, 53)	Approximately same size as in *Megasespia*	(90)–(116) mm.	Intermediate in height and size between *Pithecistes* and *Hadroleptauchenia*	Moderately wide between orbits, unreduced to reduced anteroposteriorly	Opposite anterior portion of orbit	Subhypsodont to hypsodont, expanded laterally more than in *Sespia*	Prominent
V. *Cyclopidius* (p. 296, figs. 34, 38, 40, 41)	Larger than in *Leptauchenia*, smaller than in *Hadroleptauchenia*	111–125 mm.	Intermediate in height and size between *Pithecistes* and *Hadroleptauchenia*	Moderately wide between orbits, unreduced to reduced anteroposteriorly	Opposite anterior-medial portion of orbit	Subhypsodont to hypsodont, expanded laterally	Prominent
VI. *Hadroleptauchenia* (p. 303, figs. 34, 35, 38, 40, 43, 53, 55)	Smaller than in *Pseudocyclopidius*	101–120 mm.	Moderately high, with slight to no downward slope posteriorly	Wider between orbits than in *Leptauchenia*, unreduced to reduced anteroposteriorly	Opposite anterior-medial portion of orbit	Subhypsodont to hypsodont, expanded laterally	Prominent
VII. *Pseudocyclopidius* (p. 323, figs. 36, 37, 39, 41, 43, 53)	Moderately small to small, largest of subfamily	93–145 mm.	High, with slight to no downward slope posteriorly	Wide between orbits, unreduced to reduced anteroposteriorly	Opposite anterior-medial portion of orbit	Subhypsodont to hypsodont, expanded laterally	Prominent

[1] Compare with Schultz and Falkenbach, 1940, p. 216; 1941, p. 6; 1947, p. 168; 1949, p. 85; 1950, p. 100; 1954, p. 166; 1956, pp. 392, 454; present paper, pp. 25, 194.
[2] All reduced in size; comparisons made only among the genera listed.

vidual age differentiation between the young and mature animal.]

"6. There is considerable variability in size which may be accounted for primarily as a sex difference. The somewhat larger and more heavily built skulls are probably those of males. [The present writers have not been able to distinguish sex variation of oreodonts, except to presume, as did Schlaikjer, that the narrower and lighter skulls may represent the females. In *Sespia,* and especially in *S. nitida,* there is an example of possible sex variation in that the skulls with a greater postfrontal constriction[1] may represent the females. Other examples of possible male and female skulls are noted in the *Leptauchenia, Hadroleptauchenia,* and *Pseudocyclopidius* lines. Many of these occurrences are noted in the listings.]

"A careful consideration of these facts, before new species are described, would certainly seem advisable. [The present writers would suggest considering the precise geologic occurrence of all specimens as well as the use of mature individuals for holotypes.]"

Stratigraphic Distribution

Remains of the leptauchenins have been restricted to the Brule, Gering, and Monroe Creek formations (or their approximate equivalents) in Montana, Nebraska, South Dakota, and Wyoming, and from the Sespe deposits (lower Miocene) in California. Noteworthy is the absence of leptauchenins from the fossiliferous John Day deposits of Oregon, as is indicated in chart 16 (p. 420). Previous to this report no examples of the leptauchenins had been recorded below "Zone D" (= "*Leptauchenia* beds") of the Brule, but now remains are known also from zones "A" and "C." (See chart 8, p. 228, illustrating the stratigraphic distribution of this subfamily.) Owing to the difficulties of geologic correlations of Brule deposits in different regions, the same oreodont faunal zone designations ("A," "B," "C," and "D") are used in chart 8 and throughout this paper as have been cited in the published reports[2] of the writers. It is of interest that Bump's conclusions[3] concerning the division of the Brule are the same as those published previously by Falkenbach and Schultz.[4] It should also be noted that paleosol complexes occur at the top of the deposits of each of the four oreodont faunal zones. Thus, there are now three different approaches to the correlation of the Brule in South Dakota and Nebraska, all of which are in agreement. The three methods of correlation are as follows: (1) use of paleosols,[5] (2) use of faunal (oreodont) evidence,[6] and (3) use of certain stratigraphic data.[7] The last method, however, has been difficult in the actual correlating of the Brule deposits between the different sedimentational basins in South Dakota, Nebraska, and Wyoming.

Field and laboratory studies of the upper Brule sediments of northwestern Nebraska indicate that the region was very dry and dusty during late Brule times (see p. 406 of this paper for a detailed discussion of the climatic conditions). The comparative abundance of leptauchenin remains and the scarcity of evidence of other types of oreodonts suggest that the leptauchenins were best adapted to the rigorous climate of the very late Oligocene. The specialized cursorial rhinoceroses (*Hyracodon*) also were abundant during this time, but not so much so as the leptauchenins.

Characters in Auditory Bullae

The skulls of the Leptaucheniinae all possess large, well-inflated, and rounded bullae. The bullae are the largest in all the oreodonts, i.e., in proportion to the size of the skulls. They crowd the paroccipital processes, the glenoid surfaces, the postglenoid processes, and extend forward in some instances anterior to the edges of the glenoid surfaces. The external auditory meatus is above and posterior to the bulla, necessitating a more or less vertical connection between the bulla and the external auditory meatus (in all other oreodonts a lateral tube extends from the base of the bulla to the external auditory meatus).

Actually the bulla helped to hold the condyle of the ramus in place. It limited to some degree

[1] Normally this is called a "postorbital constriction," but in the Sespiini it is not placed posteriorly enough for that.

[2] See list, p. 19.

[3] 1956, p. 429. See p. 423 of present report for detailed discussion.

[4] 1951, p. 47; see discussion, present report, p. 426.

[5] Schultz, Tanner, and Harvey, 1955, p. 4.

[6] Falkenbach and Schultz, 1951.

[7] Bump, 1956, p. 429.

CHART 9

SIZE RANGE IN THE LEPTAUCHENIINAE[a]

	No. of Examples	Skull Basal Length		P^1-M^3		Dentition P_1-M_3		M^3 AP[b]		M_3 AP	
		Range	Mean[c]	Range	Mean	Range	Mean	Range	Mean	Range	Mean
SESPIINI											
I. *Sespia*											
S. californica, Gering equivalent (Calif.)	10	—	—	32.5–35.5	34.3	36–39	37.5	—	—	—	—
S. marianae, lower Gering (Nebr., Colo.)	20	72.5	72.5	—	—	37–45.5	41.3	9.5–10.5	10.1	10. –14.5	12.5
S. nitida, upper Gering (S. Dak., Nebr., Wyo.)	59	75–83.5	80.6	40 –44.5	42.2	40.5–49	44	9.5–13.5	11.3	12.5–15	13.6
S. heterodon, Gering equivalent (Mont.)	3	—	—	—	—	—	—	—	—	—	—
S. ultima, Monroe Creek (Wyo., Nebr.)	19	81	81	42 –45	43.5	50–54.5	52	10.5–12	11.5	12 –15.5	13.8
II. *Megasespia*											
M. middleswarti, upper Gering (Nebr., Wyo.)	10	—	—	44.5–48.5	46.5	—	—	11.5–12	11.8	12 –16	14.3
LEPTAUCHENIINI											
III. *Pithecistes*											
P. tanneri, "Zone D" of Brule (Nebr., S. Dak.)	23	((89))	((89))	43.5	43.5	46	46	12	12	14	14
P. mariae, lower Gering (S. Dak., Nebr.)	10	95	95	47.5	47.5	50	50	14	14	14	14
P. altageringensis, upper Gering (Wyo., Nebr., S. Dak.)	48	—	—	(47.5)	(47.5)	53	53	14.5	14.5	16	16
P. brevifacies, Gering equivalent (Mont.)	3	(96)	(96)	46.5–47	46.8	51.5–63	57.3	—	—	—	—
P. copei, Monroe Creek (Wyo., Nebr., S. Dak.)	80	96	96	48.5–51.5	49.8	49–55	53	13 –15	14.3	15.5–17.5	16.6
IV. *Leptauchenia*											
L. harveyi, "Zone C" of Brule (Nebr., S. Dak.)	6	((90))	((90))	(46)	(46)	(49)	(49)	11.5	11.5	13.5	13.5
L. decora, "Zone D" of Brule (S. Dak., Nebr.)	202	87–105	95	44.5–53	47.6	44.5–57.5	51	11.5–16	13.5	12–18	14.8
L. martini, lower Gering (Nebr., S. Dak.)	27	101–104	102.7	56	53.3	58.5	56.2	12.5–16.5	14.7	15–19	16.6
L. parasimus, upper Gering (Wyo., Nebr.)	30	(116)	(116)	51.5–59	54.6	60–60.5	60.1	13.5–16.5	15.2	16 –20	18.3

CHART 9—(*Continued*)

	No. of Examples	Skull Basal Length		P^1-M^3		Dentition P_1-M_3		M^3 AP		M_3 AP	
		Range	Mean	Range	Mean	Range	Mean	Mean	Mean	Range	Mean
L. margeryae, Monroe Creek (Wyo., Nebr.)	53	((107))–109	107.7	49.5–61	54.8	55–(64)	58.6	13 –19	15.9	15.5–20	18.2
V. *Cyclopidius*											
C. simus, Gering equivalent (Mont.)	45	111–113	112	52 –57	54	56.5–59	57.9	—	—	—	—
C. emydinus, Gering equivalent (Mont.)	5	(118)–((125))	121.5	54.5–55.5	55	(58.5)	(58.5)	—	—	—	—
VI. *Hadroleptauchenia*											
H. eiseleyi, "Zone A" of Brule (Nebr.)	3	—	—	—	—	—	—	12.5	12.5	—	—
H. primitiva, "Zone D" of Brule (S. Dak.)	25	101–110	106.3	48 –55.6	52.9	53.5–62	57.9	14 –16	14.9	15 –17	16
H. shanafeltae, lower Gering (Nebr., S. Dak.)	60	104–115	108.5	53.5–62	57.6	59.5–66	61.7	16 –19	17.2	18 –21.5	19.1
H. densa, upper Gering (Wyo., Nebr.)	92	110–120	115.2	54 –64	61.3	66.5–72	68.7	15 –22	19.1	18 –24	21.2
H. extrema, Monroe Creek (Wyo., S. Dak.)	19	—	—	60 –65	62.3	64 –67.5	65.8	16 –19.5	18.1	18 –22	20
VII. *Pseudocyclopidius*											
P. orellaensis, "Zone A" of Brule (Wyo., Nebr.)	3	(93)	(93)	—	—	—	—	—	—	—	—
P. frankforteri, "Zone D" of Brule (S. Dak., Nebr.)	27	106–120	112.7	48.5–61.5	54.5	59 –63	60.9	13.5–17	15.3	17 –20	18.3
P. major, lower Gering (S. Dak., Nebr., Colo.)	43	121–125	123.3	59 –66.5	63.6	58.5–73	67.1	15.5–22.5	18.2	17 –24	20.5
P. lullianus, upper Gering (Wyo., Nebr.)	144	128–145	135.9	64 –74.5	68.7	67 –81	73.3	17.5–23.5	20.7	20 –31	24.5
P. lullianus expiratus, Monroe Creek (Wyo., Nebr.)	28	135	135	67 –71	69.2	65 –80	73.8	16.5–23	20.4	20 –26	23.8
P. quadratus, Gering equivalent (Mont.)											

[a] All measurements in millimeters.
[b] AP, anteroposterior.
[c] Weighted mean.

CHART 10

PROPORTIONS OF LENGTHS OF LIMBS TO BASAL LENGTHS OF ASSOCIATED SKULLS IN THE LEPTAUCHENIINAE

	Skull, Basal Length (mm.)	Humerus / B. L.	Radius / B. L.	Ulna / B. L.	Mc. III / B. L.	Femur / B. L.	Tibia / B. L.	Mt. III / B. L.
Sespia marianae								
U.N.S.M. 28420A	72.5	.94	.79	1.10	.35	.95	.97	.41
Hadroleptauchenia shanafeltae								
U.N.S.M. 1082	107	.79	—	—	.31	—	—	.33
Pseudocyclopidius major								
U.N.S.M. 1080 (male)	121	.81	.63	—	—	.82	.69	—
U.N.S.M. 1081 (female)	124	.77	.62	.83	.28	.81	.67	.29

the upward and downward movement of the ascending ramus of the mandible. This condition was apparently unique among the oreodonts. (For discussion of the internal area of the auditory bullae, see p. 463 and fig. 55.)

RANGE OF VARIATION

The apparent range of variation in the basal lengths of the skulls and in the superior and inferior dentitions within the Leptaucheniinae is shown in chart 9. The chart shows the smaller size of the Sespiini examples compared with those of the Leptaucheniini. It also indicates the trend for the forms to become larger as they occur higher in the geologic section.

There is evidence that the leptauchenins developed more rapidly during Gering times than did any other subfamily of oreodonts. The upper Gering remains are definitely larger and more advanced than those derived from the lower part of the same formation. Evolution took place at a very rapid rate, possibly as the result of the drastically changing climatic conditions during late Oligocene and early Miocene times. The leptauchenins were the only oreodonts that remained in the central Great Plains in large numbers during the late Oligocene. (See further discussion, p. 230.)

COMPARISONS OF THE LEPTAUCHENIINAE WITH THE MINIOCHOERINAE, THE OREONETINAE, AND THE MERYCHYINAE

The size range of the skulls of the Leptaucheniinae is within the same range of those of the Miniochoerinae, the Oreonetinae, and the Merychyinae. The skulls of the Leptaucheniinae differ from those of all other oreodonts in that they possess large, elongated nasal-facial vacuities. The Leptaucheniinae skulls have fan-shaped occipital regions, large nasal-facial vacuities, thin enamel on the crowns of the teeth, and shallow molar fossettes; the Miniochoerinae and the Oreonetinae have fan-shaped occipital regions, no facial vacuities, and shallow molar fossettes; and the Merychyinae have fan-shaped occipital regions, small facial vacuities, or none at all, and deep molar fossettes. All four subfamilies exhibit fan-shaped occipital regions and have large, well-inflated auditory bullae. The bullae of the Leptaucheniinae, however, are comparatively larger than those of any other oreodonts.

A. **SESPIINI,** NEW TRIBE

DESCRIPTION

The Sespiini, a new tribe of oreodonts, include the genera *Sespia* and *Megasespia.* The skulls referred to the Sespiini possess the following characters: dentitions exceptionally hypsodont (those of the Leptaucheniini, new tribe, have less hypsodont teeth); external cingulum on superior molars lacking; external styles on superior molars extremely weak or entirely absent; mesostyle present only on M^3, but weak and lost with slight wear; orbits unusually large for size of skull.

The Sespiini remains are restricted to the lower Miocene (Gering and Monroe Creek formations or their equivalents) in California, Colorado, Montana, Nebraska, South Dakota, and Wyoming.

I. **SESPIA** STOCK

Leptauchenia? (*Sespia*) STOCK, 1930, p. 38, pl. 2.

GENOTYPE: *Sespia californica* (Stock).

CHARACTERS

SKULL: Very small in size, largest example approximate length of smallest example of Leptaucheniini; basal lengths range from 72 to 83 mm., widths from 50 to 65 mm.; low degree of brachycephaly, less so than most examples of Leptaucheniini; sagittal crest moderately prominent, less so than other examples of subfamily; frontals with lesser invasion by nasal-facial vacuity, more square in outline than in other leptauchenins; orbit large, looking upward, outward, and forward; malar moderately deep below orbit; posterior border of zygomatic arch rather light, more or less confluent with external border of glenoid surface, not laterally notched as in other examples of Leptaucheniini; infraorbital foramen above P^3–P^4, high on side of face, just below border of nasal-facial vacuity; lacrimal fossa large but rather shallow; nasal-facial vacuity narrow laterally, reaching posteriorly in line with anterior border of orbit; noticeable pit or depression above premolars, because of a depressed superior anterior portion of skull; muzzle rounded at incisor border, premaxilla pinched together, giving the appearance of a beaklike extension (see fig. 31); occipital condyles small, long anteroposteriorly; posterior palate extending just posterior to M^3.

MANDIBLE: Lightest of all leptauchenins; postsymphysis below P_3; ramus moderately deep for its length; condyle light.

DENTITION: Extremely hypsodont; formula I^{2-3}_{3}, C^{1}_{1}, P^{4}_{4}, M^{2-3}_{3}; premolars somewhat crowded, set at slight angle to alveolar border; external styles of molars very weak; mesostyle on M^3 only; thin enamel on crowns, all pattern lost with small amount of wear.

LIMBS: Moderately short, somewhat robust.

MEASUREMENTS: Tables 10 and 15 (pp. 242 and 326).

ILLUSTRATIONS: Figures 31, 38–42, 53 (skulls, mandibles, and dentitions), 43 (limbs).

DISCUSSION

Sespia was originally described as a subgenus questionably referred to *Leptauchenia*, with *L.?* (*Sespia*) *californica* as the subgenotypic species. The subgenus was based primarily on the dentition, and Stock[1] reported: "External styles on upper molars less developed than in *Leptauchenia*. Styles on inner walls of lower molars feebly developed or absent. . . . *Sespia* appears to belong unquestionably to the *Leptauchenia-Cyclopidius* group. This is clearly shown by the presence of a large antorbital vacuity, compressed nasals, hypsodont dentition, and by the structural characters of the premolars. . . . *Sespia* resembles in size *Oreonetes anceps* and is smaller than *Limnenetes platyceps* of the lower Oligocene."

Schlaikjer[2] listed Stock's characters of *Sespia* and concluded: "All of these characters are prevalent in *C. heterodon* and the main distinguishing feature between these two species is one of size. . . . Since its close affinities to *C. heterodon* are now established it can be referred to the genus *Cyclopidius*, and on the basis of the known material, affords an ideal ancestral stage, structurally at least, for *C. heterodon*."

Thorpe[3] also considered *Sespia* a synonym of *Cyclopidius*. In his discussion of the species *californica* he stated: "Stock proposed to place this species in a new subgenus, *Sespia*. It is mainly a matter of personal opinion as to what characters and their degree of importance in any group constitute sufficient grounds for erecting genera and subgenera. With the exception of certain tooth variations, his subgeneric characters all fall into the genus *Cyclopidius*. The feeble development, or absence, of the normal styles on the molars is, in my opinion, a specific character. . . . Stock stated that possibly *Sespia* represented an early division of the *Leptauchenia* group tending toward *Cyclopidius*. My opinion is that *C. californicus* [= *S. californica*] is not so primitive as Stock thought. It is markedly hypsodont and has a short face, large facial vacuities, crowded premolars, and so on, all characters of the advanced *Cyclopidius* stage."

In these three reports, the fact that the den-

[1] 1930, p. 38.
[2] 1935, p. 161.
[3] 1937, pp. 241, 243.

tition of *Sespia* is more hypsodont than that of all other leptauchenins (in fact the most hypsodont of all oreodonts) was not recognized. Stock, however, did report that "the cheek-teeth have extremely long crowns." The degree of hypsodonty of the teeth was considered equivalent to that of *Cyclopidius.*

Schlaikjer's conclusions were based on material that he had referred to "*Cyclopidius*" *heterodon,* and indicates that he considered *Sespia* a synonym of *Cyclopidius.* The present writers consider the material that Schlaikjer referred to "*Cyclopidius*" *heterodon* (including his "Neotype") as referable to *Sespia nitida* (see p. 247). Otherwise most of Schlaikjer's statements are correct, since it is here considered that both species, *californica* and *heterodon,* should be referred to *Sespia.*

Thorpe's conclusions were similar to Schlaikjer's in that *Sespia* was considered to be a synonym of *Cyclopidius.* The present writers wish to enlarge on Thorpe's statement, "It is mainly a matter of personal opinion as to what characters and their degree of importance." We do not believe that the same series of characters are always of major importance within a subfamily or within the various genera of the same subfamily. Each phylogenetic line represents a problem of its own, and it is important that the worker be consistent in the consideration of the same characters within a phylogenetic line. A few examples follow. In *Ustatochoerus*[1] the various species show greater anterior retraction of the nasals as they occur higher in the geologic sequence. In the Miniochoerinae,[2] however, there is no measurable difference in the amount of anterior nasal retraction. Also in the Miniochoerinae, the genus *Platyochoerus*[3] includes skulls that are comparatively low and broad, but the skulls of the other genera and subgenera of the same family are comparably high and narrow.

In the Merychyinae, the subspecies *M. elegans bluei*[4] was established on lighter and more brachyodont dentition. It should be noted that none of the characters of a vertical sequence are apparent unless a stratigraphic control is available.

[1] Schultz and Falkenbach, 1941, figs. 8, 9.
[2] *Idem,* 1956, figs. 1, 3, 5, 6, and 8.
[3] *Idem,* 1956, p. 425.
[4] *Idem,* 1947, p. 203.

The basis of establishing *M. elegans bluei* on lighter and more brachyodont dentition is not comparable with the more hypsodont teeth and the weak styles of the molars of *Sespia.* In *M. e. bluei* a few specimens were available from one geologic unit. The more brachyodont teeth but same skull characters as in those of *M. elegans* were not observed above or below their geologic occurrence. Hence the form was established as a subspecies.

In the discussion of *Sespia,* Thorpe[5] considered the "feeble development, or absence, of the normal styles on the molars . . . a specific character." The material now at hand demonstrates that *Sespia* has these dental characters, but Thorpe did not recognize the absence of the normal styles from any of the species referable to *Sespia.*

Stock[6] thought that the size of *Sespia californica* was close to that of *Oreonetes anceps* and smaller than that of *Limnenetes platyceps.* The present writers also have noted that *O. anceps* and *L. platyceps* are of approximately the same size as *Sespia,*[7] but originally thought that the two subfamilies were not closely related. A restudy of some of the specimens referable to the Oreonetinae, however, indicates that there may be some direct relationship between this subfamily and the Leptaucheniinae. Additional leptauchenin material from oreodont faunal zones "A," "B," and "C" of the Brule also has aided much in reversing the opinion that the present writers had when they revised the Oreonetinae.[8] It now seems probable that the leptauchenins were derived from a *Limnenetes*-like ancestor.

Distribution

Five species of *Sespia* are here recorded from the lower Miocene (Gering and Monroe Creek formations or their equivalent) of California, Nebraska, Montana, South Dakota, and Wyoming. (See geologic distribution chart, p. 22.)

Summary of Species and Types

Five species and two subspecies of *Sespia* from eight lower Miocene localities are here recorded:

[5] 1937, p. 243.
[6] 1930, p. 37.
[7] Schultz and Falkenbach, 1956, table 8, p. 455.
[8] *Idem,* 1956, p. 453.

1. *S. californica* (Stock), from Ventura County, California. (Upper Sespe = in age in part to Gering Formation.)

HOLOTYPE: Anterior portion of skull and left ramus, U.C. 27720. Figures 31, 38, 40.

2. *S. marianae,* new species, from Morrill County, Nebraska; referred remains from Morrill and Banner counties, Nebraska; and tentatively referred from Weld County, Colorado. (Lower part of Gering.)

HOLOTYPE: Skull, mandible, and skeleton, U.N.S.M. 28420A. Figures 31, 38–41, 43.

3. *S. nitida* (Leidy), from South Dakota; referred remains from Washabaugh County, South Dakota; Niobrara, Goshen, and Laramie counties, Wyoming; Morrill and Banner counties, Nebraska. (Upper part of Gering.)

HOLOTYPE: Skull, A.N.S.P. 10870. Figures 31, 38.

4. *S. heterodon* (Cope), from Smith River Valley, Montana; referred from Meagher County, Montana. (Approximate Gering equivalent in age.)

HOLOTYPE: Partial right maxilla, A.M. 8131. Figures 31, 38, 39.

5. *S. ultima,* new species, from Niobrara County, Wyoming; referred from Niobrara County, Wyoming; and Sioux County, Nebraska. (Monroe Creek.)

HOLOTYPE: Skull and mandible, F:A.M. 45606. Figures 31, 38–40, 42.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

SESPIA

TOTAL AVAILABLE SPECIMENS: 101[1]

1. Sespia californica (Stock)

From the upper Sespe deposits (approximately equal in part to the Gering Formation of the Great Plains), Ventura County, California

Leptauchenia? (Sespia) californica STOCK, 1930, p. 38, pl. 2.

Cyclopidius californica (Stock): SCHLAIKJER, 1935, p. 167, fig. 11, table 5.

Cyclopidius californicus (Stock): THORPE, 1937, p. 242.

CHARACTERS

SKULL: Smallest known in genus (smallest known of leptauchenins); infraorbital foramen above anterior border of P^4. (See generic description; posterior portion of skull unknown.)

MANDIBLE: Similar to but smaller than examples of *S. marianae.* (Ascending ramus unknown.)

DENTITION: Series smallest, but typical of genus. (The incisors are unknown.)

LIMBS: Shortest in all leptauchenins.

MEASUREMENTS: Table 10 (p. 242).

ILLUSTRATIONS: Figures 31, 38, 40.

DISCUSSION

Stock originally considered this form a new subgenus, *Leptauchenia? (Sespia) californica,* and established it primarily on the weak external styles of the molars. He also pointed out that "the cheek-teeth have extremely long crowns." (See discussion, p. 239.)

Sespia californica has a well-developed M^3, and M_3 shows wear on all three lobes. In some examples of *Sespia* from the Great Plains the M^3 is present, but from others it is absent. In the latter specimens, apparently the M^3 had never developed in life. In the holotype of *S. ultima* (F:A.M. 45606) the M^3 is absent from one side of the skull and only partially developed on the other side. In the holotype of *S. marianae* (U.N.S.M. 28420A) M^3 is absent from both sides of the palate. It is interesting to note that M_3 is invariably well developed in mature examples, even when M^3 is absent from the skull of the same individual. In the cases from which M^3 is absent there seems to be some anteroposterior expansion of M^1 and M^2 to compensate for the loss of M^3, and all three lower molars show wear in the examples from which M^3's are absent.

The geologic occurrence of *S. californica,* the upper Sespe, conforms with the previous conclusions of the present writers with respect to other oreodonts from the Sespe, namely, *?Mesoreodon hesperus* (Stock),[2] and *?Desmatochoerus (Paradesmatochoerus) thurstoni* (Stock).[3]

[1] Includes 61 F:A.M. and 20 U.N.S.M. specimens.

[2] Schultz and Falkenbach, 1949, p. 151.

[3] *Idem,* 1954, p. 202.

TABLE 10

Sespia Stock and *Megasespia*, New Genus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*S. californica* (Stock)	*S. marianae*, new species	*S. nitida* (Leidy)		*S. heterodon*[b] (Cope)	*S. ultima*, new species	*M. middleswarti*,[c] new species
	Holotype U.C. 27720	Holotype U.N.S.M. 28420A	Holotype A.N.S.P. 10870	Referred F:A.M. 45611A	Holotype A.M. 21328	Holotype F:A.M. 45606	Holotype U.N.S.M. 28408
Stage of wear of teeth	(w)	(w)	(w‡‡)	(w+)	(w)	(w‡)	(w‡)
Length (incl. supraoccipital crest and incisors)	—	87	((90))	((92))	—	(96)	((108))
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	—	72.5	((81))	(83)	—	81	—
Width (max.)	—	(52.5)	(50)	(65)	—	53.5	73
Width of brain case (max.)	—	27.5	24	((33))	—	29	34
Width, interorbital (min.)	—	21.5	(24)	—	—	24	25.5
Distance from anterior rim of orbit to anterior base of C/	—	32	(36)	43	((35))	37	39
Distance from anterior rim of orbit to supraoccipital crest	—	56	(62)	—	—	66	—
Width of muzzle at infraorbital foramina	(21.5)	22	22	—	26	25	32
Width across canines	((12))	13.5	—		—	(14)	18
Length, C/–M^2 incl.	—	39	—	40	41.5	45	43
Length, C/–M^3 incl.	((40))	—[d]	—	49	—	50	53
Length, P^1–M^2 incl.	28.7[e]	35	—	34	—	40.5	39
Length, P^1–M^3 incl.	((35))	—[d]	(40.5)	43	—	45	48.5
Length, P^1–P^4 incl.	15.5	18	18.5	18	19.5	21	22
Length, M^1–M^2 incl.	12.5	16	12.5	15.5	18	18.5	18
Length, M^1–M^3 incl.	—	—	22	25	—	26	28
Width of M^3 (max.)	—	6	6.5	6.5	—	6.5	8.5
Depth of malar below orbit	—	10	10	12	—	11	11.5

TABLE 10—(*Continued*)

MANDIBULAR RAMUS	*S. californica* (Stock)	*S. marianae*, new species	*S. nitida* (Leidy)		*S. heterodon* (Cope)	*S. ultima*, new species	*M. middleswarti*, new species
	Holotype U.C. 27720	Holotype U.N.S.M. 28420A	Holotype A.N.S.P. 10870	Referred F:A.M. 45611A	Holotype A.M. 21328	Holotype F:A.M. 45606	Holotype U.N.S.M. 28408
Length (max., incl. incisors)	—	(71)	—	((81))	—	((79))	—
Length, /C-condyle incl.	—	66	—	((78))	—	74	—
Depth of jaw under coronoid	—	37	—	44	—	41	—
Depth of jaw below anterior edge of M_3	15	17	—	19	—	18	23
Length, /C–M_3 incl.	—	48.5	—	—	—	54	—
Length, P_1–M_3 incl.	((39))	45.5	—	(44)	—	50	—
Length, P_1–P_4 incl.	14.5	17	—	(17)	—	18	—
Length, M_1–M_3 incl.	—	28.5	—	27	—	32	32

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] The holotype is a partial right maxilla with P^3 (alv.)–M^1.
[c] Geologic variety, example U.N.S.M. 28410, M^1–$M^3 = 27$ mm.
[d] M^3 undeveloped.
[e] After Stock.

Ten specimens are here recorded:

HOLOTYPE

Anterior portion of skull with C/–M^3(rt.) and partial mandible with P_1–M_3(M_1 br.). (W)	U. C. 27720	From upper Sespe, South Mt., near Santa Paula, Ventura County, California; collected by U.C. field party Figured by Stock, 1930, pl. 2; Thorpe, 1937, pl. 37, figs. 1–5 This report, figures 31, 38, 40

REFERRED FROM GENERAL AREA OF TYPE (SOUTH MOUNTAIN)
(COLLECTED BY JAMES E. THURSTON)

		C.I.T.
2 SKULLS AND MANDIBLES (ATTACHED)		
Partial skull with I^2–M^3 and mandible with I_2–I_3 rt. and /C–M_3	(M)	3484
The above skull and mandible are attached and the age of the individual is at least mature. The incisor border shows no evidence of either the inferior or superior incisor ever being present.		
Partial skull and mandible	(I)	3490
2 PARTIAL SKULLS		
Anterior portion of skull with C/–dP^3–M^2	(I)	3487
Anterior portion of skull with P^1–M^3	(W+)	3488
3 MAXILLAE		
Partial right maxilla with P^4(br.)–M^3	(W‡)	3489
Partial right maxilla with P^2–M^3	(W+)	3491
Partial left maxilla with M^2–M^3(erupt.)	(I)	3492
The M^2 of the above specimen has the suggestion of a heel.		
2 MANDIBULAR RAMI		
Partial right ramus with M^1–M^3	(W)	3486
Partial left ramus with M^1(br.)–M^3(br.)	(W+)	3485
The above ramus is more robust than usual.		

2. **Sespia marianae**,[1] new species

From the lower part of the Gering Formation, Morrill County, Nebraska; referred remains from Morrill and Banner counties, Nebraska; and tentatively referred from Weld County, Colorado

DESCRIPTION

SKULL: Larger than in examples of *S. californica*; longer posterior to dentition than examples of *S. nitida*[2]; postorbital constriction slight, decidedly less than in *S. nitida*; external auditory meatus opening smaller than in other examples of genus; bulla tending to be smaller than in other forms of *Sespia*; postglenoid process with less outward slope to external border (more perpendicular) than in other species of genus; posterior palate extending posterior to M^3.

MANDIBLE: More shallow and lighter than in examples of *S. minora* and *S. ultima*; postsymphysis below midline of P_3; symphysis shorter than in examples of forms mentioned; ascending ramus not so high as in examples of *S. heterodon* or *S. ultima*.

DENTITION: Extremely hypsodont but not so much so as in examples of *S. ultima* (degree of hypsodonty greater in specimens occurring in higher portions of lower Miocene deposits, i.e., upper Gering examples of *Sespia* are more hypsodont than lower Gering forms, and Monroe Creek examples more hypsodont than upper Gering forms); formula I^3_3, P^4_4, M^{2-3}_{3}.

[1] Named in honor of Marian Schultz, wife of C. Bertrand Schultz. Marian Schultz was a member of the U.N.S.M. field parties during the collecting seasons of 1931 to 1942 inclusive and aided in the collecting and preparation of many oreodont specimens used in this series of reports, and also helped with the preparation of certain oreodont manuscripts.

[2] Possibly owing to the loss of M^3 (see discussion, p. 245.

LIMBS: Tendency to be slightly shorter than in examples of *S. nitida.*

MEASUREMENTS: Tables 10 and 15 (pp. 242 and 326).

ILLUSTRATIONS: Figures 31, 38–41, 43, 53.

DISCUSSION

Remains of *Sespia marianae* are restricted to the lower part of the Gering Formation. The holotype is one of three individuals found associated in the field, U.N.S.M. 28420A, 28420B, and 28420C. In both skulls (U.N.S.M. 28420A and 28420B) the dental series possess two molars only. There is a tendency throughout the genus for M^3 to be absent. This is also observable in the holotype of *S. ultima* (F:A.M. 45606) which has only M^1 and M^2 present on the left side of the skull and M^1, M^2, and M^3 on the right side. The right M^3, however, is much reduced in size anteroposteriorly and is not normally developed. There is no evidence of a loss of M_3's in any of the mandibular rami, even in the associated skulls from which the M^3's are absent.

The molars of *Sespia marianae* are less hypsodont than those of species that have been reported from the upper Gering and Monroe Creek. The skulls of the lower Gering species, *S. marianae,* also are somewhat smaller than those of other species from later deposits.

The U.N.S.M. specimens were collected by field parties consisting of E. L. Blue, Frank Crabill, Loren C. Eiseley, Marian and Bertrand Schultz, S. R. Sweet, Mylan Stout, Eugene Vanderpool, and associates, 1931–1938; and the F:A.M. material from Nebraska was procured by Morris F. Skinner and associates, 1955; and the specimen from Colorado was collected by Charles H. Falkenbach and associates, 1939.

Twenty specimens are here recorded:

HOLOTYPE

Skull with I^1–M^2, mandible with I_1–M_3(erupt.), and skeleton. (w)	U.N.S.M. 28420A	From lower part of Gering Formation, "30–35′ above Brule-Gering contact," U.N.S.M. Coll. Loc. MO–108, 12 mi. W. of Bridgeport, 300′ W. of road in Redington Gap on north side of Pumpkin Creek Valley, center of S. ½ sect. 14, T. 19 N., R. 52 W., North Platte River drainage, Morrill Co., Nebraska; collected by E. L. Blue, Frank Crabill, Loren Eiseley, Marian and Bertrand Schultz, and Eugene Vanderpool, 1931 Figures 31, 38–41, 43

The above skull and mandible are from a mature individual, but the upper dentition lacks M^3. There is no indication that it was present in life. The lower series, however, has an M_3 which is not completely erupted. Two additional individuals, U.N.S.M. 28420B and 28420C, were found associated with the holotype. The M^3 is also absent from skull U.N.S.M. 28420B. The latter is a mature individual. It is also noteworthy that the type of *Mesocyon geringensis* Barbour and Schultz was found 75–100′ west and some 20′ lower in the section than the holotype and associated individuals of *Sespia marianae.*

REFERRED FROM (A) MORRILL AND (B) BANNER COUNTIES, NEBRASKA; AND TENTATIVELY REFERRED FROM (C) WELD COUNTY, COLORADO

A. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM REDINGTON GAP AREA (U.N.S.M. COLL. LOC. Mo–108):

SKULL, MANDIBLE, AND SKELETAL FRAGMENTS		U.N.S.M.
Partial skull with P^3–M^2, partial mandible with M_1–M_3 and skeletal fragments . .	(w)	28420B
The M^3 in the above specimen apparently was absent when the animal died.		
DENTITION		
Fragmentary superior and inferior dentition	(w+)	28420C
The above two specimens were found associated with the holotype.		

2 SKULLS		U.N.S.M.
Inferior, anterior portion of skull with P^3–M^3	(w‡)	28427
Inferior, anterior portion of skull with P^2–M^3	(w)	28444

MAXILLA

Partial left maxilla with P^3–M^3. Figure 53 (in part)	(w+)	28448

3 MANDIBULAR RAMI

Partial right ramus with P_2(br.)–M_3	(w+)	28421
Partial right ramus with /C–P_4 rt. and M_1(br.)–M_3	(w+)	28225A
Partial right ramus with M_1(br.)–M_2	(w+)	28225B

Two of the above specimens were found associated in the field.

FROM ROUND HOUSE ROCK, BIRD CAGE GAP AREA (U.N.S.M. COLL. LOC. MO–104, 105, AND 106):

2 ASSOCIATED INDIVIDUALS

Left inferior portion of skull with C/–P^3(erupt.)–dP^4–M^2 and partial mandible with I_2–/C rt. and P_1–dP_2–P_4(erupt.)–M_3(germ)	(I)	F:A.M. 45651A
Partial mandible with I_3–/C rt. and P_1–dP_3–M_2	(I)	45651B
2 partial humeri, 3 partial radii, 4 partial ulnae, 2 partial tibiae, astragalus, 2 calcanea, ribs, and vertebrae (the limbs have not been allocated to a particular skull)		45651A–B

The above two individuals were found associated in the field "22′ above local black ash-like zone in the Gering fm. . . . 55′ above the base of the normal Gering-Whitney uncomformity."

MAXILLA AND MANDIBULAR RAMUS		U.N.S.M.
Partial right maxilla with P^4–M^3 and partial left ramus with P_3(alv.)–M_2	(w‡)	28422

3 MANDIBULAR RAMI

Right ramus with /C–P_2 alv. and P_3–M_3	(w‡+)	28446
Partial right ramus with M_2–M_3	(w‡)	28447
M_3	(w)	28456

B. FROM NORTH PLATTE RIVER DRAINAGE, BANNER COUNTY, NEBRASKA

FROM 2 MI. E. OF HUBBARD GAP (U.N.S.M. COLL. LOC. BN–101):

MAXILLA		U.N.S.M.
Partial right maxilla with P^4–M^3(br.) (M^1 alv.)	(w‡)	28445

FROM HUBBARD GAP:

MANDIBULAR RAMUS

Partial right ramus with I_1–P_1 alv. and P_2–M_3 (M_1 alv.)	(w)	28439

FROM 3 MI. W. AND 6 MI. S. OF BAYARD (U.N.S.M. COLL. LOC. BN–102):

MAXILLA

Partial left maxilla with P^2–M^1 alv. and M^2–M^3	(w+)	28443

C. TENTATIVELY REFERRED FROM SOUTH PLATTE RIVER DRAINAGE, "HIGH CHANNEL DEPOSITS" EAST OF ROCKPORT, WELD COUNTY, COLORADO

MANDIBULAR RAMUS		F:A.M.
Partial left ramus with P_1–P_3 br. and P_4–M_2(br.)	(w+)	45645

3. **Sespia nitida** (Leidy)

From deposits equivalent to the upper part of the Gering Formation, White Earth Creek, South Dakota; referred remains from Washabaugh County, South Dakota; from the Gering Formation, Niobrara, Goshen, and Laramie counties, Wyoming; and Morrill and Banner counties, Nebraska

Leptauchenia nitida LEIDY, 1869, pp. 129, 381, pl. 12, figs. 21–22. SCOTT, 1890b, pl. 16, fig. 35; 1913, figs. 200–201; 1937, figs. 5, 227–228; 1940, p. 706. SCHLAIKJER, 1935, p. 167. THORPE, 1937, p. 239, pl. 36, figs. 1-3.

Leptauchenia minora SCHLAIKJER, 1935, p. 164, pl. 41, fig. 5. THORPE, 1937, in part, p. 239, pl. 36, fig. 4.

CHARACTERS

SKULL: Approximate size of examples of *Sespia marianae* but heavier in appearance; smaller than those of *S. ultima*; exoccipital height intermediate between examples of *S. nitida* and those of *S. marianae*; greater variation of postorbital constriction (perhaps variation is indicative of sex difference, male examples being the wider); infraorbital foramen in area above posterior portion of P^3 to anterior portion of P^4; auditory bulla somewhat larger (more inflated) than examples of *S. marianae,* similar to those of *S. ultima* in this respect; posterior palate border reaching area in line with posterior border of M^3.

MANDIBLE: Intermediate in size between examples of *S. marianae* and those of *S. ultima*; postsymphysis below P_3; ascending ramus larger (higher and wider anteroposteriorly) than examples of *S. marianae,* closer to those of *S. ultima.*

DENTITION: Unworn molars intermediate in degree of hypsodonty between those of *S. marianae* and *S. ultima*; all examples possess M^3.

LIMBS: Within size range of examples of *S. marianae.*

MEASUREMENTS: Tables 10 and 15 (pp. 242 and 326)

ILLUSTRATIONS: Figures 31, 38, 40, 43.

DISCUSSION

In Leidy's[1] original description, the location of the holotype was given as ". . . on White Earth Creek, on a tributary of White River."

[1] 1869, p. 129.

The fossilization of the type specimen is similar to that of the referred specimens of *Pseudocyclopidius major* from near Eagle Nest Butte (see pp. 331–332 for discussion) which are here considered as coming from deposits equal in age to the Gering.

With one exception, previous authors have considered this species as occurring in the Brule Formation. Hay[2] questioned its occurrence as "Oligocene (Upper) or Miocene (Lower)." Actually, Hayden[3] placed the type of *S. nitida* as from "bed D of the Miocene." The additional material here referred to the species comes from the Gering Formation; in fact, no *Sespia* examples are known from the Brule.

Schlaikjer[4] considered the occurrence of *S. nitida* as in the "upper Brule," and stated: ". . . four species are now assigned to Leidy's genus *Leptauchenia.* Of these *L. nitida* [= *Sespia nitida*] is the most primitive, *L. major* [= *Pseudocyclopidius major*] the most specialized and *L. decora* is an admirable intermediate form between these two species. Although all three forms occur in the same beds such a phylogenetic arrangement is probable. *L. minora* is a small, rather specialized species which lived in early Miocene times and which probably had *L. nitida* as its direct ancestor."

Thorpe[5] agreed with Schlaikjer's assignment of geological horizons to these same forms. In a stratigraphic approach to phylogeny the lines must run vertically and not horizontally. The present writers have found evidence that the size change evident between the species *nitida, major,* and *decora* is too great to have taken place within a single geologic epoch. These species belong to three different genera, each representing an independent phylogenetic line (see chart 19, p. 43). The leptauchenins, however, developed more rapidly than some other lines of oreodonts, as is evident in the unusual change within the various lines between forms occurring in the lower and upper parts of the Gering Formation.

Both Leidy's[6] and Thorpe's[7] illustrations of

[2] 1930, p. 789.
[3] 1869, p. 17.
[4] 1935, p. 163-167, table 5, fig. 11.
[5] 1937, pp. 235, 238, 239.
[6] 1869, pl. 12, fig. 22.
[7] 1937, pl. 36, fig. 2.

S. nitida are incorrect, because they show neither the posterior portion of the postorbital process of the frontal nor the noticeable postfrontal constriction.

Scott[1] also considered the type of *S. nitida* as having been found in the Brule. An important character pointed out by Scott was: "The orbits have such a slanting position that their whole diameter is visible in the top view; their ventral boundaries, formed by the jugals, are flared outward, converting the orbits into very short tubes. No known skull, other than the types of *L. nitida,* exhibits this character." The description is accurate for this form as well as for all the material referred to *Sespia.*

Schlaikjer[2] proposed a new species, *Leptauchenia minora,* based on an immature individual from "Lower Miocene, Lower Harrison formation, approximately 200 feet above the Brule-lower Harrison contact." Schlaikjer considered all of the lower Miocene (including the Gering, Monroe Creek, and Harrison) in the area worked by him as "Lower Harrison."[3] The present writers have studied the Oligocene-Miocene stratigraphy of Goshen County as well as the large oreodont fauna (mature and immature individuals) from the area, and consider most of the fossil-yielding sediments of Miocene age as Gering. No leptauchenins have been reported from the Harrison Formation of Wyoming, Nebraska, or South Dakota. Also no oreodonts belonging to this subfamily have been found in the John Day deposits of Oregon.

Schlaikjer further stated: "... there are only three species which can be referred to *Leptauchenia.* They are *L. nitida* Leidy, *L. decora* Leidy and *L. major* Leidy. The first two are unquestionably from the upper Oligocene and the latter is either upper Oligocene or lowermost Miocene in age. The new species named above [*"Leptauchenia minora,"* based on an immature specimen] adds a fourth to the list and cannot be confused with any of the others because of its size, the compressed molars, the reduced mesostyle and the reduced incisors.

"The deciduous premolars three and four differ from those of *Cyclopidius* principally in being less molariform. The posterior portion of DP^3 is not nearly so transversely expanded and the internal cusps of DP^4 are more rounded. In *Cyclopidius* DP^4 is completely molariform."

It must be stated that the holotype of *Sespia nitida* is an old individual. The teeth are very badly worn, and the external portions of the molars are poorly preserved. Schlaikjer evidently did not consider the type specimen of *S. nitida* when naming *"L. minora,"* since he probably thought it came from the Brule. On the other hand, he suggested that the type of *Pseudocyclopidius major* may have come from either the Brule or the Miocene. (See a discussion of Leidy's work on both these forms, pp. 247 and 331.) Material here referred to *S. nitida* agrees with Schlaikjer's description of *"L. minora"* in having similar measurements, ". . . compressed molars," and "reduced mesostyle."

Although Schlaikjer stated that dP^3 and dP^4 of *"L. minora"* differ from those of *Cyclopidius* by being "less molariform," the present writers see no diagnostic difference. In immature dentition, especially in the leptauchenins, the teeth are narrow, exceptionally so with slight wear. The anterior portion of dP^3 and the "internal cusps" become expanded with wear. Schlaikjer also stated that *"L. minora"* was about one-fifth smaller than *"L. nitida."* He had no skull measurements and only an immature palate for comparison.

When all the recent evidence is considered, and with the additional material from the same collecting area as that from which Schlaikjer's specimens came, we have concluded that *"L. minora"* is a synonym of *Sespia nitida.*

Schlaikjer[4] also discussed additional specimens from the same area in Goshen County, designated the geologic occurrence as "Lower Harrison," and referred them to *Cyclopidius heterodon* Cope. The present writers have not noted characters that would separate his referred material from *Sespia nitida* or *"L. minora"* Schlaikjer. (See discussion, p. 252, under *S. heterodon.*)

Thorpe[5] accepted Schlaikjer's new species *"L. minora"* with its geological occurrence as "Lower Harrison," and stated: "It is always unsatisfactory to base species on submature specimens, such as this individual [type of *L.*

[1] 1940, p. 706.
[2] 1935, p. 164.
[3] See Schultz and Falkenbach, 1949, p. 135.
[4] 1935, p. 159.
[5] 1937, p. 239.

minora]. Schlaikjer considers this form to be the smallest so far described, or about a fifth smaller than *L. nitida*. In my opinion, based on the size of the molars and allowing for the normal growth of the skull, it is about the size of *L. decora*."

The present writers agree with Thorpe's observation as to size. Schlaikjer's "*L. minora*" and "*C.*" *heterodon* are comparable with *Sespia nitida*, and all are slightly smaller than average examples of *L. decora*.

The F:A.M. specimens from Wyoming were collected by Charles H. Falkenbach and associates, 1933, 1938, 1939, and 1942; the F:A.M. example was collected from South Dakota by Morris F. Skinner and associates, 1951; and the U.N.S.M. material, by E. L. Blue, Frank Crabill, Mylan Stout, Marian and Bertrand Schultz, and associates, 1934–1936, 1938, and 1958.

Fifty-nine specimens are here recorded:

HOLOTYPE

Partial skull with P^1–M^3(br.) (M^2 br.). (w‡‡) Female example.	A.N.S.P. 10870	From deposits equivalent in age to the upper part of the Gering Formation, White Earth Creek, White River drainage, South Dakota; collected by Hayden's Expedition, 1856 Figured by Leidy, 1869, pl. 12, figs. 21–22; Scott, 1890b, pl. 16, fig. 35; 1913, figs. 200, 201; Thorpe, 1937, pl. 36, figs. 1–3 This report, figures 31, 38

REFERRED FROM (A) WASHABAUGH COUNTY, SOUTH DAKOTA; (B) NIOBRARA, (C) GOSHEN, AND (D) LARAMIE COUNTIES, WYOMING; (E) MORRILL AND (F) BANNER COUNTIES, NEBRASKA

A. FROM WHITE RIVER DRAINAGE, 3½ MILES NORTHWEST OF WANBLEE,[1] WASHABAUGH COUNTY, SOUTH DAKOTA

		F:A.M.
Partial inferior molar	(w)	57146

B. FROM NORTH PLATTE RIVER DRAINAGE, NIOBRARA COUNTY, WYOMING

FROM WILLOW CREEK:

2 SKULLS AND MANDIBULAR RAMI

		F:A.M.
Inferior portion of skull with C/–M^3 and partial right ramus with P_1(rt.)–M_3. Figures 38, 40	(w+)	45611A
The above superior dental series has a small accessory tooth placed just posterior to the right C/.		
Partial skull with C/–M^3 and right ramus with P_3(rt.)–M_3	(w+)	45611B

SUPERIOR DENTITION AND MANDIBLE

Right and left M^3, and partial mandible with M_1(br.)–M_3	(w‡)	45611C
The above three individuals were found associated in the field.		

FROM LITTLE MUDDY CREEK:

6 MAXILLAE

Partial left maxilla with P^2–M^2	(w‡)	45613
Partial left maxilla with P^2(alv.)–M^3(br.)	(w+)	45615
Partial right maxilla with P^3–M^3	(w+)	45616
Left and right M^2	(w+)	45652
Partial right M^3	(w+)	45653
Partial left and right maxillae with P^1–M^1 (P^3 alv.)	(w+)	45649

[1] From "165′ above base of 1st white layer."

11 MANDIBULAR RAMI		F:A.M.
Partial mandible with I_1–M_3	(w)	45647
Partial right ramus with M_2–M_3	(w‡)	45617
There is a possibility that F:A.M. 45614 (left ramus, listed below) belongs to the same individual as F:A.M. 45617.		
Partial right ramus with /C–P_4	(M+)	45654
8 partial left rami with		
M_2–M_3	(w‡)	45614
M_3	(w)	45618
M_1–M_2	(w‡)	45619
M_3	(w+)	45620
P_4–M_2	(w)	45655
M_2–M_3	(w+)	45656
P_2–dP_4	(I)	45657
P_4–M_3	(M+)	45658

C. FROM NORTH PLATTE RIVER DRAINAGE, HORSECREEK BASIN, GOSHEN COUNTY, WYOMING (COLLECTED BY ERICH M. SCHLAIKJER AND ASSOCIATES, 1932–1933)

FROM BEAR CREEK MOUNTAIN AREA:

SKULL		M.C.Z.
Inferior, anterior portion of skull with I^1–dP^2–M^2	(I)	2841

The above specimen was figured by Schlaikjer, 1935, pl. 41, fig. 5; and by Thorpe, 1937, pl. 36, fig 4; and was considered to be the holotype of "*Leptauchenia minora*" by Schlaikjer (p. 164) and by Thorpe (p. 239).

SKULL AND MANDIBULAR RAMUS		
Skull with C/(br.)–dP^2–M^2 and right ramus with I_1–dP_3–M_2	(I)	2826

Figured by Schlaikjer, 1935, pl. 23, and (p. 159) referred to "*Cyclopidius*" *heterodon* (=*Sespia heterodon*).

MAXILLA		
Left maxilla with C/–M^3	(w‡)	2831

Figured by Schlaikjer, 1935, pl. 22, fig. 2, and referred to "*Cyclopidius*" *heterodon.*

FROM FOX CREEK GAP, WEST OF BEAR CREEK MOUNTAIN:

MAXILLA AND MANDIBULAR RAMUS		
Right maxilla with P^1–M^3 (M^1–M^2 alv.) and right ramus with P_1–P_4 alv. and M_1 (br.)–M_3	(w+)	2842

Figured by Schlaikjer (1935, pl. 22, figs. 3–4) and referred to "*Cyclopidius*" *heterodon* (p. 160.)

FROM 66 MOUNTAIN AREA:

SKULL AND MANDIBLE		
Partial skull with C/–M^3 and mandible (attached) with I_3(alv.)–M_3(br.)	(w+)	2849

Figured by Schliakjer (1935, pl. 22, fig. 1), and he considered the above specimen the neotype of "*Cyclopidius*" *heterodon* (p. 159).

D. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, LARAMIE COUNTY, WYOMING

FROM N. STINKING WATER:

SKULL AND MANDIBLE		F:A.M.
Anterior, inferior portion of skull with C/–M^3 and mandible with I_2–M_3	(w‡)	45612

		F:A.M.
MAXILLA		
Partial left maxilla with $C/$(br.)–dP^2–M^1(br.)	(I)	45621

FROM TREMAIN AREA:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Posterior portion of skull with M^1–M^3, partial mandible with M_1(br.)–M_3, 2 partial scapulae, 2 humeri (1 partial), radius, 2 ulnae (1 partial), 1 partial manus, 2 femora, 2 tibiae (1 partial), partial pes, astragalus, calcaneum, pelvis, vertebrae, and ribs. Male example. Figures 31, 38, 43	(w‡+)	45622
5 SKULLS AND ASSOCIATED MANDIBLES		
Anterior portion of skull with I^1–dP^3–M^2 and mandible with I_1–dP_4–M_3(germ)	(I)	57140
Skull with $C/$–P^1 br., P^2–M^3 and mandible with P_1–M_3	(w+)	57141
Partial skull with I^3–M^3 and mandible with I_2(rt.)–M_3	(w)	57142
Left maxilla with M^1 and M^3 and partial mandible with P_4–M_3	(w+)	57143
Skull with I^1–dP^2–M^2 and mandible with I_1–dP_4–M_2	(I)	57144
RAMUS AND ASSOCIATED SKELETAL ELEMENTS		
Partial left ramus with P_3(alv.)–M_3	(w‡)	57145A
Tibia		57145B
Partial pes		57145C
The above three specimens were found in one field block.		
5 SKULLS		
Partial skull (lacking contact between anterior and posterior portions) with $C/$–M^3 (br.)	(w‡)	45607
Inferior, anterior portion of skull with I^3–dP^2–M^2	(I)	45609
Inferior, anterior portion of skull with I^1–dP^1–M^1	(I)	45610
Inferior, anterior portion of skull with P^1(alv.)–P^4	(w+)	45658
Inferior, anterior portion of skull with P^1–M^2(br.)	(w)	45659
3 MAXILLAE		
Partial right maxilla with P^4–M^3	(w)	45608
Partial left maxilla with M^1–M^3 br.	(w‡)	45660
Partial right maxilla with dP^2–M^1	(I)	45650
5 MANDIBULAR RAMI		
Mandible with I_1–P_2 rt. and P_3–M_3	(w)	45644
Partial right ramus with P_4–M_3	(w+)	45661
3 partial rami with		
P_4–M_3	(w‡)	45662
P_4–M_2	(w)	45663
P_2–M_3	(w‡+)	45664
TOOTH		
Left M^3	(w)	45665

FROM 2 MI. E. OF ALBIN:

SKULL AND MANDIBLE, IMMATURE		
Anterior, inferior portion of skull with $C/$–dP^3–M^1 and partial mandible with $/C$–dP_3–M_2 (P_2 absent)	(I)	45666
MAXILLA AND MANDIBULAR RAMUS		
Partial right maxilla with $C/$–P^3 br. and P^4–M^1 and partial left ramus with P_4–M_3 br.	(w‡)	45667

E. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK BASIN, MORRILL COUNTY, NEBRASKA

FROM SW. OF BRIDGEPORT, WILDCAT RANGE:

SKULL AND MANDIBLE

Posterior portion of skull with M^1–M^3(erupt.) and partial mandible with M_1(br.)–M_3 (erupt.)	(–M)	U.N.S.M. 28409

12 MI. S. OF BRIDGEPORT:

MAXILLAE AND MANDIBLE

Partial right and left maxillae with P^2–M^3 and partial mandible with M_2–M_3	(w‡+)	28440

F. FROM NORTH PLATTE RIVER DRAINAGE, BANNER COUNTY, NEBRASKA

FROM 2 MI. N. OF WRIGHT GAP:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Posterior portion of skull with M^1–M^3, partial mandible with M_1(alv.)–M_3, partial scapula, 2 partial humeri, and vertebrae	(w+)	U.N.S.M. 28442

FROM 2 MI. NE. OF HUBBARD GAP:

SKULL

Anterior portion of skull with P^2–M^3 and left M_3	(w)	28607

F′. FROM PUMPKIN CREEK VALLEY (NORTH PLATTE RIVER DRAINAGE), S. SIDE OF HOGBACK MT., BANNER COUNTY, NEBRASKA

MAXILLA

Partial right maxilla with dP^3–M^1	(I)	U.N.S.M. 28480

4. **Sespia heterodon** (Cope)

From deposits approximately equal in age to the upper part of the Gering Formation, "Deep River" beds, Smith River Valley, Montana; referred remains from Meagher County, Montana

Cyclopidius heterodon COPE, 1878a, p. 222.

Pithecistes heterodon (Cope): COPE, 1884a, p. 559.

Cyclopidius (Pithecistes) heterodon (Cope): LOOMIS, 1925a, p. 248 (= *C. simus,* according to Loomis).

Cyclopidius (Pithecistes) decedens (Cope): MATTHEW (in part), 1899b, p. 73.

Cyclopidius simus Cope: THORPE (in part), 1937, p. 249 (*Cyclopidius heterodon* = *?C. simus,* p. 386), pl. 38, fig. 5.

CHARACTERS

SKULL: Approximately same size as examples of *S. nitida.*

MANDIBLE: (Unknown).

DENTITION: Series within size range of those of *S. nitida,* smaller than those of *S. ultima*; premolars with tendency to be more crowded than in other forms of genus; tendency for M^1–M^2 to be longer anteroposteriorly than in other examples of genus.

LIMBS: (Unknown).

MEASUREMENTS: Table 10 (p. 242).

ILLUSTRATIONS: Figures 31, 38, 39.

DISCUSSION

The type of *Sespia heterodon* (Cope) is a partial maxilla containing P^4–M^1, but the teeth are very worn and lack identifiable dental characters. The teeth are hypsodont, however, and the external styles are not present on M^1, which is a characteristic of the genus. A second example (A.M. 21328) of this species is known from Montana, and this specimen shows that both M^1 and M^2 lack the prominent styles typical of the tribe Leptaucheniini. The latter specimen also shows that only two superior incisors were present.

Schlaikjer[1] considered this a valid species, and based his conclusions on material which he collected in Wyoming and referred to *S. heter-*

[1] 1935, p. 159.

odon. He selected one of his Wyoming specimens, M.C.Z. 2849, as a "neotype" of this species, but the present writers have referred all this material to *S. nitida* (see p. 250).

Most of the species of the Montana leptauchenins appear to be valid although many have been placed in synonymy, namely, *brevifacies* Cope (see p. 268); *emydinus* Cope (p. 302); and *incisivus* Scott (p. 298). In the discussions of the various species in this report, the differences between the Montana forms and their nearest affinities from Nebraska or Wyoming are noted. There appears to be some evidence that the Montana forms evolved independently from those of the central Great Plains. Hence it is to be suspected that, when a more complete skull of *S. heterodon* is known, it will differ even more specifically from examples of *S. nitida* from South Dakota, or from the other species.

Thorpe[1] disagreed with Schlaikjer and considered *Sespia heterodon* to be a synonym of *Leptauchenia* (*Cyclopidius*) *simus* and stated, "Cope defined the species [as being] smaller than *C. simus*, with the styles on M^1 much smaller than in that species; in fact, he stated that there are no distinct vertical ribs." Thorpe also pointed out that Cope thought that "it is quite possible that it [*C. heterodon*] does not belong to this genus [*Cyclopidius*]." It is of interest that Cope, as early as 1894, recognized the possibility of a new genus for forms with this type of teeth. Stock[2] was the first to establish a subgenus, *Leptauchenia?* (*Sespia*), for oreodonts with teeth of this type.

Thorpe[3] concluded: "The teeth [of *S. heterodon*] are much worn in the type, but it is certainly a small animal, with its P^4 and M^1 longer than wide. In fact, the lateral compression of M^1 is more pronounced than in any of the other species, which may indicate that we have here a female of *C. simus*." The present writers have not observed that sex variation includes the lack of external styles on the molars. The teeth may be lighter in a female example, but not more compressed.

In a discussion of the genus *Pithecistes*, Matthew[4] stated, "*Pithecistes decedens* is the permanent and *P. heterodon* [= *Sespia heterodon*] probably the milk dentition of a smaller species of *Cyclopidius*." The present writers believe the type of the species of *decedens* to be referable to *Cyclopidius simus* (p. 298). The type of *Sespia heterodon*, however, has permanent teeth as has been established by various workers since the time of Matthew's report.

Two specimens are here recorded:

HOLOTYPE

Partial right maxillary with P^3 (alv.), P^4–M^1. (w)	A.M. 8131	Lower Miocene deposits, Smith River Valley, Montana; collected by J. C. Isaac. Figured by Schlaikjer, 1935, pl. 26, fig. 2; Thorpe, 1937, pl. 38, fig. 5 This paper, figures 31, 38, 39

REFERRED FROM 7 MILES SOUTHEAST OF FORT LOGAN, ON EAST SIDE OF SMITH RIVER, MONTANA (COLLECTED BY C. C. MOOK AND ASSOCIATES)

PARTIAL SKULL		A.M.
Anterior portion of skull with I^2(alv.)–M^2	(w)	21328

[1] 1937, p. 254.
[2] 1930, p. 38.
[3] 1937, p. 255.
[4] 1899a, p. 73, footnote 2.

5. **Sespia ultima**,[1] new species

From the Monroe Creek Formation, Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; and Sioux County, Nebraska

DESCRIPTION

SKULL: Longer and higher than other examples of *Sespia*; infraorbital foramen in area above and between P^3–P^4; auditory bulla equal to examples of *S. nitida*.

MANDIBLE: Ramus deeper in posterior half than in other species of genus.

DENTITION: Most hypsodont molars of all leptauchenins; compressed laterally but not so much so as in other examples of Sespiini.

LIMBS: (Unknown).

MEASUREMENTS: Tables 10 and 15 (pp. 242 and 326).

ILLUSTRATIONS: Figures 31, 38–40, 42, 53.

DISCUSSION

Sespia ultima represents the latest known species in the phylogeny of the genus. The skulls are longer and wider than those of the Gering species, and the molars are more hypsodont.

The holotype of *S. ultima* from the Monroe Creek Formation has a basal length approximately equal to examples of *Pithecistes tanneri* from oreodont faunal "Zone D" of the Brule. Superficially the skulls are similar in appearance. The molars of *S. ultima* are much more hypsodont and lack the prominent external styles which are found in *P. tanneri* and the other species of *Pithecistes*.

The F:A.M. material was collected by Charles H. Falkenbach and associates, 1934–1936, 1939, and 1943.

Nineteen specimens are here recorded:

HOLOTYPE

Partial skull with C/–M^3, and mandible with I_2–I_3 rt. and /C–M_3. (M+)	F:A.M. 45606	From Monroe Creek Formation, Muddy Creek, North Platte River drainage, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1934 Figures 31, 38–40, 42

The dentition of the above type indicates that the left M^3 was not present in life, yet the right M^3 was present but reduced in its anterior-posterior length. The crown of M^3 is a single lobe with a weak heel which is more apparent at its base. The lower dentition, however, has well-developed third molars.

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; AND (B) SIOUX COUNTY, NEBRASKA

A. FROM NORTH PLATTE RIVER DRAINAGE, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

4 SKULLS AND MANDIBLES		F:A.M.
Partial skull with I^3(br.)–M^3 and partial mandible with P_1–M_3	(w)	45605
From above the white layer on Muddy Creek, W. of bridge.		
Partial skull with P^2–P^3 rt. and P^4–M^3 and mandible with P_1–M_3	(w‡)	45623
The above specimen comes from the high exposure, 1 mi. E. of the bridge.		
Partial skull with dP^2–dP^4–M^3(germ) and mandible (attached) with P_1–dP_2–M_2 .	(I)	45624
The above specimen comes from above the white layer, W. of the bridge.		
Partial skull with I^2(rt.)–M^3 and partial mandible with I_1–/C rt. and P_1–M_3 (P_3br., P_4 absent, no contact between premolars and molars). Figure 53	(w‡)	45625
SKULL		
Inferior, anterior portion of skull with P^2–M^3	(w)	45643

[1] Indicating the last geologic occurrence of *Sespia*.

3 MAXILLAE AND MANDIBULAR RAMI		F:A.M.
Left maxilla with C/(br.)–M^2 and partial mandible with I_1–M_3	(w)	45626
Right maxilla with P^1–M^3(br.) and partial right ramus with P_4–M_3	(w‡)	45668
Partial left and right maxillae with M^2–M^3 and partial right ramus with M_3	(w‡)	45669
6 MANDIBULAR RAMI		
Partial right ramus with M_2–M_3	(w+)	45627
5 partial left rami with		
P_1–M_1(br.)	(w)	45628
/C(br.)–P_4	(w)	45629
M_1–M_3(br.)	(w+)	45630
I_3–M_1	(w)	45670
M_1–M_2	(w+)	45671
3 DETACHED TEETH		
M_1	(w‡)	45672
M_1	(w‡)	45673
M_3	(w+)	45674

B. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, HEAD OF WARBONNET CREEK, SIOUX COUNTY, NEBRASKA (COLLECTED BY O. A. PETERSON, 1904)

MAXILLA		C.M.
Partial left maxilla with P^3–M^2	(w+)	1293

II. **MEGASESPIA**, NEW GENUS

GENOTYPE: *Megasespia middleswarti*, new species.

DESCRIPTION

SKULL: Moderately small in size; basal length 89± mm., width 73 mm.; larger than examples of *Sespia* from same geologic zone, approximately same size as *Leptauchenia decora*; brachycephalic; sagittal crest moderately prominent; higher than examples of *Sespia*, slight downward slope posteriorly; brain case inflated laterally (depressed vertically); frontals moderately narrow between orbits, unreduced anteroposteriorly; nasals wider transversely than those of *Sespia;* orbit large and looks upward, outward, and forward; lacrimal fossa prominent but not deep, expanded along malar; zygomatic arch moderately light, inferior border with marked upward rise posteriorly; shallow pit or depression on face above premolars; auditory bulla inflated, but much less so than in *L. decora*.

MANDIBLE: Moderately robust; postsymphysis in region below P_3; ramus rather deep; inferior border of ramus with gradual posterior downward trend; ascending ramus moderate anteroposteriorly.

DENTITION: Hypsodont, less so than in examples of *Sespia* but more so than in all other leptauchenins; formula, $I\frac{3}{3}$–$M\frac{3}{3}$; premolars not overcrowded; superior molars lacking prominent external styles similar to examples of *Sespia*; molars with less transverse compression than in *Sespia*.

LIMBS: Larger than those of *Sespia*. (Known from partial pes only.)

MEASUREMENTS: Table 10 (p. 242).

ILLUSTRATIONS: Figures 31, 38, 40, 53 (skulls, rami, and dentition), 43 (limbs).

DISCUSSION

The genus *Megasespia* includes forms with broad, flat skulls. The $M\frac{2}{2}$ and $M\frac{3}{3}$ are very hypsodont, but less so than in *Sespia;* the superior molars lack the prominent external styles that are also absent from *Sespia*. There is less transverse compression of the superior molars than in examples of *Sespia*.

DISTRIBUTION

Remains of *Megasespia* are not well distributed. One species is here recorded from the lower Miocene (upper part of the Gering) of Nebraska and Wyoming. A geologic variety is reported from the lower portion of the Gering of Nebraska. (See geologic distribution chart, p. 228.)

SUMMARY OF SPECIES AND TYPE

One species and one geologic variety of *Megasespia* from three lower Miocene (Gering) localities are here recorded:

1. *M. middleswarti*, new species, from Banner County, Nebraska; referred from Morrill County, Nebraska; and Laramie County, Wyoming. (Upper part of Gering.)

HOLOTYPE: Skull and left ramus, U.N.S.M. 28408. Figures 31, 38, 40, 43.

1a. *M. middleswarti*, geologic variety, from Scotts Bluff, Morrill, and Banner counties, Nebraska. (Lower part of Gering.)

EXAMPLE: Partial right ramus, U.N.S.M. 28410.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

MEGASESPIA

TOTAL AVAILABLE SPECIMENS: 14[1]

1. **Megasespia middleswarti**,[2] new species

From the upper part of the Gering Formation, Banner County, Nebraska; referred remains from Morrill County, Nebraska; and Laramie County, Wyoming; and a geologic variety from the lower part of the Gering Formation, Scotts Bluff, Morrill, and Banner counties, Nebraska

Leptauchenia decora Leidy: THORPE (referred only), 1937, p. 235, pl. 35, figs. 2–5.

DESCRIPTION

SKULL: Largest in the Sespiini, approximately equal in size to examples of *Pithecistes copei* (from the Monroe Creek) and *Leptauchenia decora* (from the Brule); lower (more depressed) than those of *P. copei* or *L. decora*; comparatively lower than all examples of *Sespia*; more brachycephalic than examples of *Sespia* or *Pithecistes*, comparable with *L. decora*; sagittal crest thin but moderately high, more prominent than in *Sespia*; brain case expanded laterally; narrowest portion of nasals wider than those in *Sespia* and *Pithecistes*; orbit much larger than examples of *P. copei* or *L. decora*; infraorbital foramen above posterior border of M^3; nasal-facial vacuity posteriorly aligned with anterior border of orbit (see generic description).

Thorpe[3] referred the specimen U.N.S.M. 2–26–7–32SP (= U.N.S.M. 28408), which is now the holotype of *M. middleswarti*, to *Leptauchenia decora* and considered it as the "plesiotype" (p. 235) and "PLT" (p. 380) of that species. The hypsodont dentition and the Miocene (Gering) occurrence of the type of *M. middleswarti* evidently were not considered by Thorpe sufficient evidence to separate it from *L. decora*, which has much less hypsodont dentition and is typically Oligocene (upper Brule) in age.

The U.N.S.M. specimens were collected by C. Bertrand Schultz and associates, 1934, 1937, and 1950; and the F:A.M. example was collected by Charles H. Falkenbach and associates, 1938.

Ten specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3, partial left ramus with P_3(br.)–M_3, and partial pes. (w‡)	U.N.S.M. 28408	From the upper part of the Gering Formation, S. and E. of LaGrange, Wyoming; in Banner County, Pumpkin Creek drainage, Nebraska; collected by C. B. Schultz and associates, 1932 Figured by Thorpe, 1937, pl. 35, figs. 2–5 This report, figures 31, 38, 40, 43

[1] Includes 13 U.N.S.M. specimens and 1 F:A.M. specimen.

[2] Named in honor of Mr. Tom Middleswart, Department of Roads, State of Nebraska, Bridgeport, Nebraska. Mr. Middleswart also is a Research and Field Associate in the Division of Vertebrate Paleontology, University of Nebraska State Museum. Mr. Middleswart and his wife Gwen have found many new fossil localities during the past 30 years and have donated a large number of specimens to the Nebraska State Museum.

[3] 1937, pp. 235, 380.

Thorpe[1] considered this holotype as a plesiotype and a plesiolectotype of *Leptauchenia decora* Leidy. Thorpe used U.N.S.M. field catalogue number 2-26-7-32S.P. for this specimen when he published.

REFERRED FROM (A) LARAMIE COUNTY, WYOMING; AND (B) MORRILL COUNTY, NEBRASKA

A. FROM NORTH PLATTE RIVER DRAINAGE, TREMAIN AREA, HORSE CREEK BASIN, LARAMIE COUNTY, WYOMING

SKULL		F:A.M.
Partial skull with M^2–M^3 br.	(w+)	45675

B. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

From U.N.S.M. Coll. Loc. MO–108:

THREE ASSOCIATED INDIVIDUALS		U.N.S.M.
Partial left and right maxillae with C/(br.)–M^3(P^1 alv.) and partial mandible with /C–M_2(br.)(P_1 br.)	(w‡)	28477A
Partial left and right maxillae with M^1–M^3 and partial mandible with P_4(br.)–M_3	(w)	28477B
Partial right maxilla with M^3	(m+)	28477C
Skull and skeletal fragments		28477A–C

From Redington Gap Area:

SKULL, IMMATURE		
Partial skull with C/–dP^2–M^2(germ)	(i)	28455

MAXILLA		
Partial right maxilla with M^2–M^3	(w+)	28241

From Black Hank's Canyon (U.N.S.M. Coll. Loc. MO–109):

MANDIBULAR RAMUS		
Partial left ramus with M_2–M_3 (lacking heel)	(w‡)	28209

From Wildcat Ridge (Collected by S. R. Sweet):

MANDIBULAR RAMUS		
Partial left ramus with P_4–M_3	(w)	28441

1a. Geologic Variety

From the lower part of the Gering Formation, Scotts Bluff, Morrill, and Banner counties, Nebraska

Discussion

The following example is incomplete and does not possess diagnostic characters to separate it from examples of *M. middleswarti.* It did, however, occur in deposits of earlier age than did examples of that species.

Three specimens are here recorded:

EXAMPLE

Partial right maxilla with P^3–M^3. (w‡+)	U.N.S.M. 28478	From lower part of Gering Formation, "15–25 ft. above Brule-Gering contact," 1 mi. W. of U.N.S.M. Coll. Loc. SF–101 (Scotts Bluff National Monument), North Platte River drainage, Scotts Bluff County, Nebraska; collected by Charles Irons, U.N.S.M. field party, 1932

[1] 1937, p. 235.

REFERRED FROM (A) MORRILL AND (B) BANNER COUNTIES, NEBRASKA

A. FROM U.N.S.M COLL. LOC. MO–104, PUMPKIN CREEK DRAINAGE, MORRILL COUNTY, NEBRASKA

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with M_1(alv.)–M_2	(M)	28479

B. FROM U.N.S.M. COLL. LOC. MO–110, NORTH PLATTE RIVER DRAINAGE, BANNER COUNTY, NEBRASKA

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with M_2–M_3	(W+)	28410

B. LEPTAUCHENIINI, NEW TRIBE

DESCRIPTION

The Leptaucheniini, a new tribe of oreodonts, include those forms of leptauchenins that have the following characters: less hypsodont dentitions than those of the Sespiini; M^1 and M^2 with external cingulae (also partially developed on M^3); prominent external styles on molars; mesostyles on molars overlapping, becoming more prominent with wear. The genera *Pithecistes, Leptauchenia, Cyclopidius, Hadroleptauchenia,* and *Pseudocyclopidius* are included in the new tribe.

The Leptaucheniini are known from oreodont faunal zones "A," "B," "C," and "D" of the Brule, and from the Gering and Monroe Creek formations or from deposits of equivalent age in Montana, Nebraska, South Dakota, and Wyoming.

Scott[1] proposed the "LIMNENETES-LEPTAUCHENIA-CYCLOPIDIUS Tribe," and discussed the phylogenetic charts which previously had been proposed by Loomis and Thorpe. Both of these latter workers considered *Limnenetes* or the "Limnenetes-line" as the ancestral line of the leptauchenins. Scott stated: "Considering first Thorpe's hypothesis of the actual and direct descent of *Leptauchenia* from *Limnenetes,* we should note that the problem is twofold: (1) Could *Leptauchenia* have been derived from some such form as *Limnenetes,* assuming that the time involved was sufficient for such derivation? (2) Did the time between lower Chadron and upper Brule suffice for so great a change? . . . but, admitting that there was the needed time, there is no obvious reason why *Leptauchenia* might not have been derived from *Limnenetes.*"

[1] 1940, p. 689.

This problem has been discussed by the present writers,[2] whose conclusions were: ". . . the present writers fail to see any direct connection between the two forms [*Limnenetes* and *Leptauchenia*]. It seems reasonable to suspect that the ancestors of the leptauchenins would have possessed some indications of [nasal-] facial vacuities." Now that the characters of the leptauchenins are much better known, there is a strong possibility of a direct relationship between the Leptaucheniinae and the Oreonetinae. At least the two subfamilies could have been derived from a common ancestor. The dentitions of *Oreonetes* are very similar to those of the lower and middle Brule examples of the Leptaucheniini, and the inflated bullae of both groups are very much alike.

III. PITHECISTES COPE

Pithecistes COPE, 1878a, p. 219. SCOTT, 1890b, pl. 15, figs. 20, 21; 1937, p. 365.

Cyclopidius Cope: MATTHEW (in part), 1899b, p. 73. THORPE (in part), 1937, p. 249.

Cyclopidius (*Pithecistes*) (Cope): LOOMIS, 1925a, p. 248.

GENOTYPE: *Pithecistes brevifacies* Cope.

DESCRIPTION

SKULL: Moderately small in size; ranging in basal lengths from 89 to 96 mm., widths from 62 to 66 mm.; approximate length of examples of *Megasespia*; subbrachycephalic, similar to examples of *Sespia,* higher than those of *Megasespia;* facial region shortened anteroposteriorly; sagittal crest moderately prominent, higher than in *Sespia,* with slight downward slope posteriorly; brain case elongated, inflated vertically, somewhat compressed transversely;

[2] 1956, p. 453.

frontals narrow between orbits, reduced anteroposteriorly; nasals moderately light, more so than in examples of *Megasespia*; orbits small, looking mostly outward, less upward and forward than those of *Megasespia*; malar extremely deep, deeper than examples of *Sespia* or *Megasespia*; inferior border of zygoma rising noticeably to sharply posteriorly; infraorbital foramen in area above anterior border of P^3 to anterior border of P^4; lacrimal fossa shallow; posterior border of nasal-facial vacuity from opposite posterior to anterior border of orbit to midline of orbit; slight facial pit or depression above premolars; muzzle narrow; auditory bulla medium to large in size, elongated anteroposteriorly.

MANDIBLE: Moderately light to moderately robust; postsymphysis in area below P_3; ramus moderately deep to deep; inferior border with slight to noticeable downward slope posteriorly; ascending ramus moderately high; ramus foreshortened anteriorly.

DENTITION: Subhypsodont to hypsodont; premolars not overcrowded; expanded laterally, more so than in examples of *Sespia* and *Megasespia*; external styles of molars prominent, decidedly more so than in the Sespiini.

LIMBS: Light and small. (Known from partial femur only.)

MEASUREMENTS: Table 11 (p. 260).

ILLUSTRATIONS: Figures 32, 38, 40, 53 (skulls, mandibles, and dentitions).

DISCUSSION

Matthew,[1] Schlaikjer,[2] and Thorpe[3] all considered *Pithecistes* to be a synonym of *Cyclopidius*. Loomis[4] considered *Pithecistes* to be a subgenus of *Cyclopidius*, which might be expected inasmuch as the genotypic species, *P. brevifacies*, was founded by Cope[5] on the partial mandible of an aged individual (A.M. 8129). He based the new genus *Pithecistes* mainly on his misinterpretation of the number of lower incisors present. (See discussion, p. 268.) Later Cope[6] again discussed the characters of *Pithecistes* and stated: "The diagnosis of the genus is as follows: Inferior premolars three; incisors one. Canine caniniform, masticating with the superior canine. No diastema. Symphysis coossified." With the exception of the incorrect statement on the number of incisors, this description could be applied to any oreodont.

Matthew[7] reported that "*Pithecistes* was distinguished by Cope from *Cyclopidius* by: (1) lower incisors reduced to one on each side; (2) canine [lower] not incisiform; (3) P_1, absent . . . Careful comparison and more complete removal of the matrix show that: (1) the alveoli of two small incisors are present on each side; (2) the canine, mistaken by Cope for an incisor, is present and worn to a stump; (3) the first pre-molar, mistaken for canine by Cope, is present and caniniform; (4) there are no distinctions whatsoever from *Cyclopidius simus* except those due to the age of the individual."

The material now available shows that the oreodonts from the central Great Plains representing this phylogenetic line had mandibles with a foreshortened anterior portion similar to the holotype of *Pithecistes brevifacies,* the genotypic species.

It is now apparent that the holotype of *P. brevifacies* has three incisors despite previous interpretations of the dentition. The dental formula has no real bearing on the generic description, and thus a new description of the species has been proposed by the present writers.

DISTRIBUTION

The remains of *Pithecistes* are not widely distributed. Five species are here recorded from the upper Oligocene and lower Miocene (orodont faunal "Zone D" of Brule Formation and the Gering and Monroe Creek formations, or equivalents) of Montana, Nebraska, South Dakota, and Wyoming. (See geologic distribution chart, p. 228.)

SUMMARY OF SPECIES AND TYPES

Five species of *Pithecistes* from four upper Oligocene and eight lower Miocene localities are recorded:

1. *Pithecistes tanneri,* new species, from Morrill County, Nebraska; referred remains from Morrill, Sioux, and Scotts Bluff counties,

[1] 1899b, p. 73.
[2] 1935, p. 167, table 5.
[3] 1937, p. 241.
[4] 1925a, p. 248.
[5] 1878a, p. 219.
[6] 1884a, p. 557.
[7] 1899b, p. 73, footnote 2.

TABLE 11

Pithecistes Cope. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*P. tanneri*, new species	*P. mariae*, new species	*P. altageringensis*, new species	*P. brevifacies* (Cope)	*P. copei*, new species
	Holotype U.N.S.M. 28451	Holotype F:A.M. 45633	Holotype F:A.M. 45638	Holotype A.M. 8129	Holotype F:A.M. 34483
Stage of wear of teeth	(w^+)	(M^+)	(w^+)	(w‡‡)	(w‡)
Length (incl. supraoccipital crest and incisors)	(100)	(108)	—	—	107
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	((89))	95	—	—	96
Width (max.)	65	(66)	—	—	(65)
Width of brain case (max.)	25.5	31	—	—	31
Width, interorbital (min.)	(31)	32	—	—	31
Distance from anterior rim of orbit to anterior base of C/	—	33	—	—	37
Distance from anterior rim of orbit to supraoccipital crest	(65)	77	—	—	87
Width of muzzle at infraorbital foramina	(23)	32	—	—	32
Width across canines	—	—	—	—	16.5
Length, C/–M^3 incl.	—	54.5	—	—	55
Length, P^1–M^3 incl.	43.5	47.5	(47.5)	—	48.5
Length, P^1–M^4 incl.	19.5	21	(20)	—	21
Length, M^1–M^3 incl.	25.5	30	28	—	28
Width of M^3 (max.)	10	11	11.5	—	12.5
Depth of malar below orbit	13	15	—	—	16.5
MANDIBULAR RAMUS			Referred F:A.M. 45635		
Stage of wear of teeth			(w‡)		
Length (max., incl. incisors)	(86)	—	—	—	—
Length, /C-condyle incl.	81	77.5	—	—	((85))
Depth of jaw below anterior edge of M_3	19	21	26	26	24
Length, /C–M_3 incl.	49	50.5	57.5	56	52.5
Length, P_1–M_3 incl.	46	50	53	51.5	49
Length, P_1–P_4 incl.	18.5	20	20.5	18	17.5
Length, M_1–M_3 incl.	29	30.5	33	34.5	33.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

Nebraska; and Fall River County, South Dakota. (Oreodont faunal "Zone D" of Brule Formation.)

Holotype: Skull and mandible, U.N.S.M. 28451. Figures 32, 38, 40.

2. *Pithecistes mariae*, new species, from Shannon County, South Dakota; referred remains from Morrill County, Nebraska. (Lower part of Gering, or equivalent.)

Holotype: Skull, mandible, and skeletal elements, F:A.M. 45633. Figures 32, 38, 40.

3. *Pithecistes altageringensis,* new species, from Niobrara County, Wyoming; referred remains from Niobrara, Converse, and Laramie counties, Wyoming; Morrill County, Nebraska; and Shannon and Washabaugh counties, South Dakota. (Upper part of Gering, or equivalent.)

HOLOTYPE: Anterior portion of skull, F:A.M. 45638. Figures 32, 38.

4. *Pithecistes brevifacies* Cope, from "Deep River," Montana; referred remains from Meagher County, Montana. (Approximately equal in age to upper part of Gering.)

HOLOTYPE: Partial mandible, A.M. 8129. Figures 32, 40.

5. *Pithecistes copei,* new species, from Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; Sioux County, Nebraska; and Shannon County, South Dakota. (Monroe Creek.)

HOLOTYPE: Skull and mandible, F:A.M. 34483. Figures 32, 38, 40.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

PITHECISTES

TOTAL AVAILABLE SPECIMENS: 168[1]

1. Pithecistes tanneri,[2] new species

From oreodont faunal "Zone D" of the Brule Formation, Morrill County, Nebraska; referred remains from Morrill, Sioux, and Scotts Bluff counties, Nebraska; and Fall River County, South Dakota

DESCRIPTION

SKULL: Smallest of genus; postorbital constriction variable, lesser constriction perhaps representing male examples; nasal-facial vacuity extending posteriorly to align with anterior portion of orbit; zygomatic arch with gradual upward slope posteriorly; auditory bulla slightly smaller than in examples of *P. copei.*

MANDIBLE: Lightest and smallest of genus; posterior symphysis below midline of P_4.

DENTITION: Subhypsodont; lightest of genus; less lateral expansion than other species of genus; lower premolars more crowded than uppers; P_2–P_3 set at a slight angle to alveolar border.

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 260).

ILLUSTRATIONS: Figures 32, 38, 40, 53.

DISCUSSION

Pithecistes tanneri, new species, is the earliest known species of the genus. The remains of this form are restricted to oreodont faunal "Zone D" of the Brule. Although leptauchenins are now recorded from all four faunal zones "A," "B," "C," and "D" of the Brule, no evidence of this genus has been discovered from the faunal zones below "D."

It is of interest that examples of *P. tanneri* include those with either deep or comparatively shallow malar bones. Perhaps this variation is sexual, with the deeper malars representing male examples.

It is noteworthy that William W. Fry of St. Louis, as a graduate student at Columbia University, prepared a report (unpublished) for one of William King Gregory's vertebrate paleontology classes, naming a new species based on a skull and mandible, A.M. 27017. This same specimen is here referred to *P. tanneri.* Fry's proposal for a new species was based largely on the dental characteristics of the crowns. As is stated above in the present report, the enamel on the crowns of the cheek teeth of the leptauchenins was lost with little wear, and thus the dental characteristics were soon lost.

It is here considered that *P. tanneri* from "Zone A" of the Brule gave rise to *P. mariae* from the lower part of the Gering.

The U.N.S.M. material was collected by C. Bertrand Schultz and associates, 1931–1934, 1936, 1937, 1950, 1951, 1956; the F:A.M. specimen was collected by Morris F. Skinner and associates, 1956.

Twenty-three specimens are here recorded:

[1] Includes 143 F:A.M. and 20 U.N.S.M. specimens.

[2] Named in honor of Mr. Lloyd Tanner, Associate Curator of Vertebrate Paleontology and Coordinator of Field Parties, University of Nebraska State Museum. Mr. Tanner has aided the writers in many ways in the preparation of the oreodont manuscript.

HOLOTYPE

Skull with C/(rt.)–M^3 and mandible with /C–M_3. (w+)	U.N.S.M. 28451	From oreodont faunal "Zone D" of Brule Formation, "70 feet above lowest ash of Whitney," North Platte River drainage, U.N.S.M. Coll. Loc. MO–111, 6–7 mi. E. and S. of Broadwater, Morrill County, Nebraska; collected by S. R. Sweet, Marian and Bertrand Schultz, and associates, 1936 Figures 32, 38, 40

REFERRED FROM (A) MORRILL, (B) SCOTTS BLUFF, AND (C) SIOUX COUNTIES, NEBRASKA; AND (D) FALL RIVER COUNTY, SOUTH DAKOTA

A. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

From Pumpkin Creek Valley, Wildcat Ridge, SW. of Bridgeport (Collected by S. R. Sweet, 1931):

SKULL AND MANDIBLE		A.M.
Partial skull with C/–M^3 (P^1 alv.) and mandible with I_1–M_3	(w)	27017

From Pumpkin Creek Valley, U.N.S.M. Coll. Loc. MO–104:

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with I_1–P_2 alv. and dP_3–M_2	(I)	28485

From Pumpkin Creek Valley, U.N.S.M. Coll. Loc. MO–107:

MANDIBLE		
Partial mandible with I_1–M_3	(w)	28481

From Pumpkin Creek Valley, U.N.S.M. Coll. Loc. MO–108:

SKULL		
Anterior portion of skull with C/(br.)–M^3	(w)	28482

From Pumpkin Creek Valley, 1/2 Mi. E. of U.N.S.M. Coll. Loc. MO–108:

MANDIBULAR RAMUS		
Partial right ramus with /C–M_2(br.)	(w+)	28243

From E. and S. of Broadwater, U.N.S.M. Coll. Loc. MO–111 (Same Locality as Holotype):

2 SKULLS		
Anterior portion of skull with I^1–I^3 alv. and C/–M^3	(w‡+)	28483
Anterior portion of skull with P^1–M^3	(w+)	28484

B. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

From Scotts Bluff Monument Area, U.N.S.M. Coll. Loc. SF–101:

SKULL AND MANDIBLE		U.N.S.M.
Partial skull with C/(rt.)–M^3 and partial mandible with /C(rt.)–M_3. Figure 53 (in part)	(w)	28492

From 7 Mi. W. of U.N.S.M. Coll. Loc. SF–101:

SKULL AND MANDIBLE — U.N.S.M.

Skull with I^3–M^3 and mandible with $/C$–M_3 . . . . (w‡) 28491

FROM 6 MI. E. OF LYMAN, U.N.S.M. COLL. LOC. SF–102:

SKULL AND MANDIBLE

Inferior portion of skull with P^1–P^3 br. and P^4–M^3 and partial mandible with P_3–M_1 rt. and M_2–M_3 . . . . (w‡) 28432

C. FROM NORTH PLATTE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM DUE NORTH OF MITCHELL:

SKULL AND MANDIBLE — F:A.M.

Partial skull with I^2(rt.)–M^3 and partial mandible with M_1–M_3(br.) (M_2 br.) . . . (w) 45677

FROM 12 MI. N. OF THE CITY OF SCOTTSBLUFF:

SKULL AND MANDIBLE — U.N.S.M.

Parts of skull with P^2(rt.)–M^3 and partial mandible with P_1(rt.)–M_3 . . . . . . (w‡) 28488

SKULL, IMMATURE — F:A.M.

Partial skull with dP^4–M^2 . . . . (I) 45676

C′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–22:

2 SKULLS AND MANDIBLES — U.N.S.M.

Partial skull with P^1–M^3 and mandible (attached) with P_1(br.)–M_3 . . . . (w) 28489
Partial skull with P^4–M^3 and partial mandible with M_1–M_3. . . . . (w+) 28490

FROM U.N.S.M. COLL. LOC. SX–27:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with P^2(br.)–M^3, partial mandible with P_2–M_3, partial femur, partial tibia, and fragments . . . . (w+) 28486

FROM U.N.S.M. COLL. LOC. SX–43:

SKULL

Partial skull with P^4–M^1 br. and M^2–M^3 . . . . (w‡⁺) 28487

D. FROM WHITE RIVER DRAINAGE, 7 MILES NORTHWEST OF SLIM BUTTE, FALL RIVER COUNTY, SOUTH DAKOTA

2 ASSOCIATED INDIVIDUALS

Partial skull with P^4(br.)–M^3, partial mandible (attached) with M_2–M_3, partial humerus, partial radius, partial ulna, and fragments . . . . (w‡) F:A.M. 45568A

MAXILLA

Partial left maxilla with dP^2–dP^4 . . . . (I) 45568B

The above two specimens were found associated in the field.

SKULL AND MANDIBLE (ATTACHED)

Partial skull with P^1–M^3 and mandible with P_1–P_3 rt. and P_4–M_3 . . . . (M+) 45678

2 SKULLS

Partial skull with $C/$–M^3 (P^1 rt.) . . . . (w+) 45679
Partial skull with $C/$–M^3 (P^1 rt.) . . . . (w+) 45680

2. **Pithecistes mariae,**[1] new species

From lower Miocene deposits, approximately equal in age to the lower Gering Formation, Shannon County, South Dakota; referred remains from the lower part of the Gering Formation, Morrill County, Nebraska

DESCRIPTION

SKULL: Slightly larger and higher and more robust than in examples of *Pithecistes tanneri;* malar either shallow or comparatively deep below orbit (possibly sexual variation, deep examples being male); zygomatic arch having inferior border with sharper posterior rise than in examples of *P. tanneri,* less sharp than those of *P. copei;* nasal-facial vacuity aligning posteriorly almost to midline of orbit; auditory bulla larger and slightly more elongated than in examples of *P. tanneri,* not so long vertically as those of *P. copei;* infraorbital foramen in area above posterior portion of P^3.

MANDIBLE: Moderately robust; heavier than in examples of *P. tanneri;* postsymphysis below anterior portion of P_4; ramus deeper than in examples of *P. tanneri;* ascending ramus high and wide anteroposteriorly, higher and wider than in *P. tanneri.*

DENTITION: Hypsodont, more so than in examples of *P. tanneri,* less so than in all species of the Sespiini; premolars not overcrowded; series longer than in examples of *P. tanneri.*

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 260).

ILLUSTRATIONS: Figures 32, 38, 40.

DISCUSSION

Pithecistes mariae is readily distinguished from the Oligocene *P. tanneri* by its more robust skull and more hypsodont dentition. The geologic sequence is from *P. tanneri* ("Zone D") to *P. mariae* and in turn giving rise to *P. altageringensis* from the upper Gering.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1942, 1950, 1954; and the U.N.S.M. examples, by C. Bertrand Schultz and associates, 1931, 1938.

Nine specimens are here recorded:

HOLOTYPE

Skull with I^3–M^3, mandible with P_1–M_3, and partial femur. (M+)	F:A.M. 45633[2]	From lower Miocene deposits equal in age to lower part of Gering Formation, "25′ above base of 1st white layer," S. end of Sheep Mt., White River drainage, Shannon County, South Dakota; collected by Thomas Lucas, Morris F. Skinner, and Morris F. Skinner, Jr., 1950 Figures 32, 38, 40

REFERRED FROM (A) SHANNON COUNTY, SOUTH DAKOTA, AND (B) SIOUX AND (C) MORRILL COUNTIES, NEBRASKA

A. FROM "ABOVE BASE OF FIRST WHITE LAYER," WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM S. END OF SHEEP MT., "23′ ABOVE BASE OF FIRST WHITE LAYER":

2 SKULLS AND MANDIBLES, IMMATURE

		F:A.M.
Partial skull with C/–dP^3–M^2 (P^1–P^2 alv.) and mandible (attached) with P_1–dP_3–M_2	(I)	45681
Skull with C/–dP^2–M^2 and mandible with /C(br.)–dP_3–M_2	(I)	45682

FROM SE. CORNER OF SHEEP MT., "26′ ABOVE BASE OF FIRST WHITE LAYER":

[1] Named in honor of Mrs. Marie Skinner, who has helped her husband, Morris F. Skinner, Sr., in the collecting of the South Dakota and Nebraska oreodont material, and also aided the writers in many ways in the preparation of the oreodont manuscript.

[2] Other fragments of limbs are associated with this number but they are too large for this genus and species.

SKULL		F:A.M.
Inferior, anterior portion of skull with C/–M^3	(W)	45683

B. FROM SIOUX COUNTY, NEBRASKA

FROM S. FACE OF CHALK BUTTE, ATABERY RANCH:

SKULL AND MANDIBLE		
Partial skull with P^1–M^3 and mandible (attached) with I_3–M_3	(M+)	45684
SKULL		
Skull with I^1–I^2 alv. and I^3–M^3	(M+)	45685

Morris Skinner has restudied the geology at this locality and now considers that the specimens were derived from the Whitney rather than the Gering.

C. FROM MORRILL COUNTY, NEBRASKA

FROM REDINGTON GAP AREA:

MAXILLA		U.N.S.M.
Partial right maxilla with P^4–M^3	(W)	28493

FROM 12 MI. S. OF BRIDGEPORT:

MANDIBULAR RAMUS		
Partial left ramus with P_1–P_2 alv. and P_3(rt.)–M_3	(W+)	28411

FROM $1\frac{1}{4}$ MI. W. AND $1\frac{1}{2}$ MI. N. OF REDINGTON, PUMPKIN CREEK DRAINAGE:

MANDIBULAR RAMUS		
Partial right ramus with I_3–dP_2–M_2	(I)	28494

3. **Pithecistes altageringensis,** new species

From upper part of Gering Formation, Niobrara County, Wyoming; referred remains from Niobrara, Converse, and Laramie counties, Wyoming; and Morrill County, Nebraska; and from Gering equivalent, Shannon and Washabaugh counties, South Dakota

DESCRIPTION

SKULL: Slightly larger and heavier than in examples of *P. mariae;* infraorbital foramen above midline of P^3; palate wider. (Known from inferior, anterior portion of skull.)

MANDIBLE: More robust than in examples of *P. mariae;* postsymphysis below P_3; extremely sharp rise anteriorly (to symphysis) of inferior border from below anterior portion of M_2; ascending ramus high, higher than in examples of *P. mariae.*

DENTITION: Formula I_1^1–M_3^3 (may vary in number of upper incisors); hypsodont; series tending to be longer and slightly more hypsodont than in examples of *P. mariae.*

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 260.)

ILLUSTRATIONS: Figures 32, 38, 40.

DISCUSSION

The proposed new species, *P. altageringensis,* is known only from incomplete specimens. The indications are that the skull, mandible, and dentition are larger than those of *P. mariae.* The marked difference is in the shape of the inferior, anterior border in the ramus, giving the symphysis an abbreviated appearance like that of a bulldog. This particular characteristic appears also in the holotype of *Pithecistes brevifacies.*

The marked differences in the mandibular symphyses of examples of *P. altageringensis* and those of *P. mariae* make doubtful the direct relationship between these two species. More complete examples of *P. altageringensis* are needed in order to solve this problem.

The F:A.M. specimens from Wyoming were collected by John Lynch, Everett De Groot, Gene Roll, Nelson J. Vaughan, and Charles H. Falkenbach, 1933, 1937–1939, and 1942; the F:A.M. examples from South Dakota, by Morris F. Skinner and associates, 1951; and the U.N.S.M. material was collected by C. Bertrand Schultz and associates, 1934.

Forty-seven specimens are here recorded:

HOLOTYPE

Inferior, anterior portion of skull with P^1(alv.)–M^3. (W+)	F:A.M. 45638	From upper part of Gering Formation, Little Muddy Creek, North Platte River drainage, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933 Figures 32, 38

REFERRED FROM (A) NIOBRARA, (B) GOSHEN, AND (C) LARAMIE COUNTIES, WYOMING; (D) MORRILL COUNTY, NEBRASKA; AND (E) SHANNON, AND (F) WASHABAUGH COUNTIES, SOUTH DAKOTA

A. FROM NORTH PLATTE RIVER DRAINAGE, LITTLE MUDDY CREEK, NIOBRARA COUNTY, WYOMING

2 SKULLS		F:A.M.
Inferior, anterior portion of skull with M^1–M^3	(M+)	45688
Anterior portion of skull with P^1–dP^2–M^2	(I)	45689
13 MAXILLAE		
7 right maxillae with		
M^1(br.)–M^3	(M)	45690
P^2–M^3 (P^4 br.)	(W)	45691
P^3–M^1(br.)	(W+)	45692
P^3–M^3	(M+)	45693
P^1(br.)–M^3(erupt.)	(−M)	45694
P^4–M^3	(W)	45695
M^1–M^3	(W)	45696
6 left maxillae with		
P^2–P^3	(W+)	45697
P^3–M^3	(M+)	45698
dP^2–dP^4	(I)	45699
P^4–M^1(br.)	(M)	45687
C/–M^3	(W‡)	56700
M^1–M^3(br.)	(W+)	56701
4 MANDIBLES		
4 partial mandibles with		
P_1(rt.)–M_3 (P_4 rt.)	(W)	45603
P_3–P_4 erupt. and M_1–M_3	(−M)	56702
/C–M_3. Figures 32, 40	(W‡)	45635
I_1–I_3 rt. and P_1–M_3(br.) (P_2–P_3 br.)	(W)	56703
20 MANDIBULAR RAMI		
11 partial right rami with		
P_1–dP_2–dP_4	(I)	56704
P_2–dP_3–dP_4	(I)	56705
I_2–I_3 alv. and /C–M_1(rt.) (P_1 br.)	(M+)	56706
dP_3–M_1	(I)	56707
M_1–M_3	(W)	56708
M_2–M_3	(W)	56709
P_4–M_2	(W+)	56710
M_1–M_2	(W)	56711
dP_4(br.)–M_1	(I)	56712
/C–dP_3–M_1	(I)	56713
P_3–P_4	(M+)	56714

		F:A.M.
9 partial left rami with		
P_1(rt.)–dP_4–M_1 (P_2 rt. and dP_4 br.)	(I)	56715
dP_4(br.)–M_1	(I)	56716
P_1(br.)–dP_3–M_1(br.) (P_2 alv.)	(I)	56717
P_3–dP_4–M_1	(I)	56718
dP_3–dP_4	(I)	56719
P_4–M_3(br.) (M_1 alv.)	(W)	56720
M_1–M_2	(W+)	56721
M_3	(W+)	56722

B. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, S. SIDE OF 66 MOUNTAIN, GOSHEN COUNTY, WYOMING

MANDIBULAR RAMUS		F:A.M.
Partial left ramus with P_3(rt.)–M_3	(W+)	56723

C. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, LARAMIE COUNTY, WYOMING

FROM E. OF TREMAIN:

MAXILLA		F:A.M.
Partial right maxilla with P^4–M^2	(W+)	56724

FROM NEAR ALBIN ROAD:

2 MANDIBULAR RAMI		
Partial right ramus with P_2(rt.)–M_3(br.)	(W)	56725
Partial left ramus with P_3–M_3 br.	(W)	56726

D. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, MORRILL COUNTY, NEBRASKA

FROM REDINGTON GAP AREA:

SKULL		U.N.S.M.
Inferior, anterior portion of skull with C/–P^2 rt. and P^3–M^3	(M+)	28495

FROM 12 MI. S. OF BRIDGEPORT:

SKULL AND MANDIBLE		
Parts of skull with P^1–P^2 and P^4–M^3 and partial right ramus with M_1(br.)–M_3	(M+)	28496

E. FROM WHITE RIVER DRAINAGE, 3 MILES BELOW PORCUPINE CREEK, SHANNON COUNTY, SOUTH DAKOTA

MAXILLA		F:A.M.
Left maxilla with P^1–P^2 alv. and P^3–M^3	(W)	37231

F. FROM WHITE RIVER DRAINAGE, 3½ MILES NORTHWEST OF WANBLEE[1] WASHABAUGH COUNTY, SOUTH DAKOTA

MAXILLA		F:A.M.
Partial left maxilla with P^3–M^3	(W‡)	57147

[1] From "165′ above base of 1st white layer."

4. **Pithecistes brevifacies** Cope

From deposits approximately equal in age to the upper part of the Gering Formation, "Deep River," Montana; referred from Meagher County, Wyoming

Pithecistes brevifacies COPE, 1878a, p. 219, pl. 27, figs. 2, 3. SCOTT, 1890b, pl. 15, figs. 20, 21.

Pithecistes facies COPE, 1888, p. 1079, pl. 27, figs. 2, 3 (name *"facies"* appears on plate only; typographical error).

Cyclopidius brevifacies (Cope): SCHLAIKJER, 1935, p. 160.

Pithecistes breviceps [= *brevifacies*] (Cope): LOOMIS, 1925a, p. 248.

Cyclopidius simus (Cope): MATTHEW (in part), 1899b, p. 73. LOOMIS (in part), 1925a, p. 248. THORPE (in part), 1937, p. 251, figs. 178, 179.

Cyclopidius loganensis KOERNER, 1940, p. 856, pl. 4, fig. 3.

CHARACTERS

SKULL: Same approximate length as, but narrower in facial region than, example of *P. copei;* nasal-facial vacuity extending posteriorly to align with midline of orbits; infraorbital foramen above anterior portion of P^3.

MANDIBLE: Moderately deep; postsymphysis below P_3; anterior portion foreshortened. (See generic description.)

DENTITION: Formula I^2_3–M^3_3; hypsodont; premolar crowded.

LIMBS: (Unknown). (Koerner included with his type of *"C. loganensis,"* "Skull and jaws, parts of six cervical vertebrae and various limb bones." The elements were not described, and the present writers did not find such elements with the skull and mandible.)

MEASUREMENTS: Table 11 (p. 260).

ILLUSTRATION: Figures 32, 40.

DISCUSSION

The dental formula for the type of *Pithecistes brevifacies* reported by Cope[1] was: "I.1; C.1; Pm.3; M.3. The single incisor of each side is weak and easily lost; and there is on one side only a small alveolus for a minute second incisor. It is therefore probable that in some individuals the incisor formula is 2."

Matthew[2] reported, "Careful comparisons and more complete removal of the matrix show that: (1) the alveoli of two small incisors are present on each side; (2) the canine, mistaken by Cope for an incisor, is present and worn to a stump; (3) the first pre-molar, mistaken for canine by Cope, is present and caniniform."

Thorpe,[3] in discussing the above quotation, stated: ". . . these same teeth are C_1, P_1, P_4, M_3. This specimen may perhaps be later than the other species [of *Cyclopidius*] and may have had but two incisors on each side. . . . In any event, they must have been tiny, and we have no way at present of determining the number and size of the incisors. Cope's incisor is the true canine, while his canine is P_1."

Possibly the type had lost an incisor. On the other hand it is possible that on the right side of the mandible there is I_1–I_2 alv., I_3 (the latter is twisted out of place, with space for the /C) questionably /C alv., P_1–P_4, M_1 alv., and M_2–M_3; the left side has I_1–I_3 alv., /C, and P_1 rt. Other specimens of *Pithecistes* have the full complement, I_1–M_3. (See figs. 39, 40.) Evidently Thorpe had considered that the two incisors differ in position and the I_3 on the right side differs from the larger tooth on the left side. Since the type is an aged individual, possibly a tooth was lost in life and the alveolus was closed.

Without regard to the number of incisors present, *Pithecistes brevifacies* is a valid species and well named. Cope recognized the abbreviated anterior portion of the ramus evident throughout the phylum and exaggerated in the later forms of the genus.

Loomis[4] concluded that *P. breviceps* (= *brevifacies*), *Cyclopidius* (*P.*) *decedens*, and *C.* (*P.*) *heterodon* were synonyms of *C. simus.*

Koerner[5] proposed a new species, *"Cyclopidius loganensis,"* from Montana (here referred to *Pithecistes brevifacies*) and compared his specimen with various species of *Cyclopidius. Cyclopidius simus* was the only form from Montana with which comparison was made. Admittedly other authors had placed *Pithecistes brevifacies* in synonymy.

Koerner's specimen Y.P.M. 13951 (holotype of *"C. loganensis"*) has not been completely prepared. Many important characters as well as the crowns of the dentition are still embedded in matrix.

[1] 1878a, p. 219.
[2] 1899b, p. 73.
[3] 1937, p. 251.
[4] 1925a, p. 248.
[5] 1940, p. 857.

Three specimens are here recorded:

HOLOTYPE

Partial mandible with I_1–I_2 alv. and I_3–M_3 (M_1 alv.). (w‡‡)	A.M. 8129	From deposits approximately equal in age to the upper part of Gering Formation, "Deep River," Montana; collected by J. C. Isaac, 1877 Figures 32, 40

REFERRED FROM (A) TYPE AREA; AND (B) MEAGHER COUNTY, MONTANA

A. FROM "DEEP RIVER," MONTANA

MANDIBULAR RAMUS

		A.M.
Right ramus with P_1–M_3	(w)	8119

B. FROM MEAGHER COUNTY, MONTANA (COLLECTED BY H. E. KOERNER, 1935 and 1937)

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		Y.P.M.
Skull with I^2–M^3, mandible (attached) with I_1(alv.)–M_3, and skeletal elements. Figured by Koerner, 1940, pl. 4, fig. 5 . . . . Designated as holotype of *Cyclopidius loganensis*.	(w‡$^+$)	13951

5. **Pithecistes copei**,[1] new species

From the Monroe Creek Formation, Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; Sioux County, Nebraska; and Shannon County, South Dakota

DESCRIPTION

SKULL: Approximate size of that of examples of *Pithecistes brevifacies;* larger than in other examples of genus; zygomatic arch with abrupt rise of malar posterior to orbit; malar very deep below orbit; infraorbital foramen in area above anterior border of P^3; orbit looking mostly outward, slightly upward and forward; nasals very light; bulla well inflated, more so than in other species of genus, and long anteroposteriorly.

MANDIBLE: Similar to that of examples of *P. brevifacies.*

DENTITION: Formula I^3_3–M^3_3; wider transversely than other examples of genus; P^1 at angle to alveolar border; external styles of superior molars well developed; P_1–P_4 crowded, set at angle to alveolar border; inferior premolars not aligned with molars, alveolar border curving inward anteriorly.

LIMBS: (Unknown).

MEASUREMENTS: Table 11 (p. 260).

ILLUSTRATIONS: Figures 32, 38, 40, 53.

DISCUSSION

The proposed new species *P. copei* is the latest, geologically, known species of the genus. It has developed a more laterally expanded dentition and a more inflated bulla. The increase in lateral expansion of the dentition is a trend in the phylogenetic lines of the leptauchenins. Specimens of *P. copei* also differ from examples of *P. brevifacies* in weight of teeth. The difference is consistent when leptauchenins from Montana are compared with similar forms from the same geologic period in the Great Plains.

In size, examples of *P. copei* are close to those of *Sespia ultima* from the same formation. Their dentition, however, differs considerably. *Sespia ultima* has exceptionally hypsodont teeth, with the superior external styles almost completely lacking.

The Wyoming F:A.M. specimens were collected by Charles H. Falkenbach and associates, 1933–1942; and the F:A.M. examples from Nebraska and South Dakota, by Morris F. Skinner and associates, 1941 and 1950.

[1] Named in honor of E. D. Cope who described the genus *Pithecistes.*

Eighty specimens are here recorded:

HOLOTYPE

Skull with I^3(alv.)–M^3 (C/ rt.) and mandible with I_2–P_4 rt. and M_1–M_3. (w‡)	F:A.M. 34483	From Monroe Creek Formation, Muddy Creek, North Platte River drainage, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933 Figures 32, 38, 40

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING; (B) SIOUX COUNTY, NEBRASKA; AND (C) SHANNON COUNTY, SOUTH DAKOTA

A. FROM NORTH PLATTE RIVER DRAINAGE, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

3 ASSOCIATED INDIVIDUALS		F:A.M.
Anterior, inferior portion of skull with I^2–M^3	(w‡)	56727A
Anterior, inferior portion of skull with C/–dP^2–M^2	(I)	56727B
Partial left maxilla with M^1–M^3	(w‡)	56727C
Mandible with I_1–M_3	(w‡)	56727D
Partial mandible with P_1–dP_2–M_2	(I)	56727E
Partial mandible with P_1–P_4 rt. and M_1–M_2(rt.)	(w)	56727F

All the above specimens were found associated in the field. However, there is no certainty that the upper series belongs to a particular lower dentition. More than three individuals may be represented.

SKULL AND MANDIBLE, IMMATURE		
Inferior, anterior portion of skull with I^2(alv.)–dP^2–M^2 and partial mandible with I_1–dP_2–M_2	(I)	56728

5 SKULLS		
5 anterior, inferior portions of skulls with		
P^1(alv.)–dP^2(br.)–M^1	(I)	56729
C/–dP^2–dP^4	(I)	56730
P^1(alv.)–dP^2–M^1	(I)	56731
C/–dP^3–M^2.	(I)	56732
C/–M^3. Figure 53	(w)	56733

3 MAXILLAE AND MANDIBULAR RAMI		
Partial left maxilla with dP^2(rt.)–M^2 and partial right ramus with P_1–dP_2–M_2(br.) (P_3 alv.)	(I)	56734
Partial right and left maxillae with C/–M^3 and partial mandible with I_1–/C br. and P_1–M_1(br.)	(–M)	56735
Partial left maxilla with I^3–dP^1–M^1(br.) and mandible with I_1–dP_2–M_2	(I)	56736

14 MAXILLAE		
8 right maxillae with		
C/(br.)–M^2(br.)	(w)	56737
P^4(br.)–M^3 (M^1 br.)	(w+)	56738
P^4–M^3	(M)	56739
M^1–M^3	(w+)	56740
M^1–M^3	(w‡)	56741
M^1–M^2	(w+)	56742
M^2–M^3	(w)	56743
C/–dP^2–M^2(erupt.)	(I)	56744

6 partial left maxillae with		F:A.M.
P^2–M^3	(W‡)	56745
P^3–M^3	(W)	56746
P^4–M^3	(W)	56747
P^1–dP^2–M^1	(I)	56748
dP^3–M^1	(I)	56749
C/–dP^2–M^2(br.) (P^1 rt.)	(I)	56750

6 MANDIBLES

6 partial mandibles with		
I_3–dP_2–M_2(br.)	(I)	56751
I_2–M_3	(W+)	56752
I_3–P_4 rt. and M_1–M_3	(W)	56753
I_3–P_3 rt. and dP_3–M_2	(I)	56754
/C–P_1 rt. and P_2–M_3	(W+)	56755
I_1–M_3	(W)	56756

12 MANDIBULAR RAMI

6 partial right rami with		
I_1–P_1 rt. and P_2(alv.)–M_3(br.) (P_3 alv.)	(W+)	56757
P_2(alv.)–M_1	(M)	56758
M_1–M_2	(W‡)	56759
M_1–M_3	(M+)	56760
P_1–dP_3–M_2	(I)	56761
dP_4–M_1	(I)	56762
6 partial left rami with		
P_2(alv.)–dP_3–M_1	(I)	56763
M_1–M_2	(W)	56764
/C–dP_2–M_2	(I)	56765
dP_4–M_2	(I)	56766
P_1–dP_3–M_2(br.)	(I)	56767
P_4(br.)–M_3(br.)	(W+)	56768

B. FROM UPPER PART OF MONROE CREEK FORMATION, NORTH PLATTE RIVER DRAINAGE, TUNNEL HILL LOCALITY, LEDINGHAM RANCH, SIOUX COUNTY, NEBRASKA

AT LEAST 6 ASSOCIATED INDIVIDUALS

4 PARTIAL SKULLS

		F:A.M.
Inferior, anterior portion of skull with P^1(alv.)–M^3	(–M)	45631A
Inferior, anterior portion of skull with C/–P^3 rt. and P^4–M^3	(W‡)	45631B
Fragment of skull with M^1	(W)	45631C
Inferior, anterior portion of skull with dP^2–M^2	(I)	45631D

3 PARTIAL MAXILLAE

Partial right maxilla with P^4–M^1 br. and M^2–M^3	(W)	45631E
Partial left maxilla with M^1–M^2(br.)	(–M)	45631F
Partial left maxilla with dP^3–M^2 br.	(I)	45631G

15 MANDIBULAR RAMI

Partial symphysis with P_1	(W)	45631H
10 partial right rami with		
P_4–M_2 alv. and M_3(br.)		45631I
P_3(br.)–M_3(br.) (P_4–M_2 alv.)	(W+)	45631J
M_2–M_3	(W)	45631K
dP_2–dP_4 br. and M_1–M_2	(I)	45631L
M_1–M_2(br.)	(W+)	45631M

		F:A.M.
M_3	(w+)	45631N
M_2	(w)	45631T
M_3	(w‡)	45631U
M_3	(M)	45631V
5 partial left rami with		
M_2–M_3	(w‡+)	45631O
/C and P_4–M_3 (M_1–M_2 br.)	(w+)	45631P
I_1 rt. and M_2(br.)–M_3	(w‡+)	45631Q
P_2–P_4 erupt. and M_1–M_2(erupt.)	(I)	45631R
P_4(br.)–M_2	(w)	45631S

The above specimens were all found associated in the field. All are poorly preserved and incomplete, and it is not possible to be certain which maxilla goes with which ramus.

MAXILLA

Partial left maxilla with C/–M^2	(w+)	56769

MANDIBULAR RAMI

Partial mandible with I_1–P_4 rt. and M_1–M_3	(w+)	56770
Partial left ramus with P_1(rt.)–M_3(erupt.) (P_3–P_4 erupt.)	(–M)	56771
Partial left ramus with dP_3–M_3(germ)	(I)	56772

C. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 1½ MI. S. OF LARGE EXPOSURES AT MOUTH OF PORCUPINE CREEK CANYON:

2 MAXILLAE

		F:A.M.
Partial right maxilla with P^3(br.)–M^3	(w‡+)	56773
Partial right maxilla with P^3–M^3	(w‡+)	56774

3 MANDIBULAR RAMI

Partial right ramus with M_1–M_3	(w‡)	56775
Partial right ramus with P_4–M_3(br.)	(w‡+)	56776
Partial left ramus with M_1	(w+)	56777

Morris Skinner, the collector of the above four specimens, considered the geologic occurrence as being "near top of pink clay with small nodules and below ?Harrison or Monroe Creek-like bluffs." The material appears to be from the Monroe Creek Formation, perhaps the lower portion, since it was associated with examples of both *Pithecistes copei* and *Pseudocyclopidius expiratus*, two species that are typical of the Monroe Creek.

FROM WOUNDED KNEE CREEK:

MAXILLA

		A.M.
Right maxilla with P^1–M^3	(M)	27865

V. LEPTAUCHENIA LEIDY

Leptauchenia LEIDY, 1856a, p. 88.

Cyclopidius (*Chelonocephalus*) THORPE, 1921b, p. 415, figs. 4, 5; 1937, p. 256.

GENOTYPE: *Leptauchenia decora* Leidy.

GENERIC CHARACTERS

SKULL: Small size, basal lengths ranging from 90 to 107 mm., widths from 60 to 90 mm.; mesocephalic to brachycephalic; sagittal crest moderately high posteriorly; brain case moderately expanded laterally, depressed posteriorly (causing sagittal crest to be high posteriorly); frontals wide between orbits, from unreduced to reduced anteroposteriorly; orbit small, comparable with examples of *Pithecistes*, looking outward, forward, and upward; malar from moderately deep to deep below orbit; zygomatic arch with confluent rise posterior to inferior border; infraorbital foramen above anterior portion of P^3; lacrimal fossa shallow; nasal-facial vacuity extending to a point above anterior portion of M^3; slight depression or pit on face above premolars; auditory bulla inflated, long vertically.

MANDIBLE: Moderately light; postsymphysis in area below posterior portion of P_2 to P_3; ramus shallow, slightly deeper than earlier (geologic) examples of *Pithecistes;* inferior border of ramus with gradual downward slope posteriorly; ascending ramus moderately high.

DENTITION: Subhypsodont; formula,[1] I^3_3–M^3_3; premolars not crowded, set more or less straight with alveolar border; external styles of molars prominent, slightly less so in Oligocene forms, more so in Miocene examples; series less hypsodont in those from Oligocene than from Miocene.

LIMBS: Lightly built; small in size, larger than in examples of *Sespia,* smaller and lighter than those of *Hadroleptauchenia* and *Pseudoleptauchenia.*

MEASUREMENTS: Tables 11 and 15 (pp. 260 and 326).

ILLUSTRATIONS: Figures 33, 38, 40, 41, 53 (skulls, mandibles, and dentition); 43 (skeletal elements).

DISCUSSION

The genus *Leptauchenia* was the first-named genus of the Leptaucheniinae. Now available are large series with stratigraphic data for all the subfamily. Remains of *Leptauchenia* are now known to occur in zones "C" and "D" of the Brule, Gering, and Monroe Creek formations. Examples of *L. decora* are the most common of the leptauchenins from "Zone D" of the Brule.

The genus *Cyclopidius* was named by Cope[2] to include Miocene leptauchenins that possessed two incisors only. (See discussion, p. 296.) With the now available material, there is no doubt that the *Leptauchenia* phylum extended into the Miocene. The *Cyclopidius* phylum, based on narrower and lighter dentitions, seems to be restricted to the Miocene of Montana. There remains the question whether all *Leptauchenia* examples had three incisors or all those of *Cyclopidius* had two. As has been noted, the incisors are very small and no doubt easily lost in life; if so, the alveolus of a lost incisor would fill up with bone.

Matthew[3] considered *Pithecistes* a synonym of *Cyclopidius.* Thorpe[4] named a new subspecies, *Cyclopidius schucherti.* Loomis[5] concluded that Cope's *Brachymeryx* and *Pithecistes* and Thorpe's *Chelonocephalus* were all synonyms of *Cyclopidius.* Schlaikjer[6] recognized only the genera *Leptauchenia* and *Cyclopidius. Thorpe*[7] concluded that *Brachymeryx, Pithecistes,* and *Sespia* (Stock) were all synonyms of *Cyclopidius.* Koerner[8] followed Thorpe except that he did not mention Stock's *Sespia.*

The present writers consider the following two genera valid: *Sespia Stock* (p. 239) and *Pithecistes* Cope (p. 258). (See respective discussions for details.)

DISTRIBUTION

The remains of *Leptauchenia* are not widely distributed. Five species are here recorded from the Upper Brule ("Zones C–D"), Gering, and Monroe Creek of Nebraska, South Dakota, and Wyoming. (See geologic distribution chart, p. 228.)

SUMMARY OF SPECIES AND TYPES

Five species of *Leptauchenia* from 10 upper Oligocene and nine Miocene localities are here recorded:

1. *Leptauchenia harveyi,* new species, from Sioux County, Nebraska; referred remains from Shannon County, South Dakota. (Oreodont faunal "Zone C" of Brule Formation.)

HOLOTYPE: Skull and mandible, U.N.S.M. 28450. Figures 33, 38, 40.

2. *Leptauchenia decora* Leidy, from the "Valley of the White River," South Dakota; referred remains from Jackson, Fall River, Pennington, Shannon, and Washabaugh coun-

[1] Thorpe, 1937, p. 234, gave the formula "I^3_3". The basis for this is questionable. The specimens he named as "genotypes and genoparatypes" do not have incisors. One of his "plesiotypes" of *Leptauchenia decora,* here considered the type of *Megasespia middleswarti,* has three incisors. None of the specimens here referred to *Leptauchenia* has the incisors.

[2] 1878a, p. 221.

[3] 1899b, p. 72.

[4] 1921b, p. 415; 1937, p. 256.

[5] 1925a, p. 248.

[6] 1935, p. 167.

[7] 1937, p. 241.

[8] 1940, p. 839.

TABLE 12

Leptauchenia Leidy and *Cyclopidius* Cope. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*L. harveyi*, new species	*L. decora* Leidy	*L. martini*, new species		*L. parasimus*, new species	*L. margeryae*, new species	*C. simus* Cope	*C. emydinus* Cope
	Holotype U.N.S.M. 28450	Referred[b] F:A.M. 45502	Holotype F:A.M. 45571A[c]	Referred F:A.M. 45571B	Holotype F:A.M. 34485	Holotype F:A.M. 45632	Holotype A.M. 8116	Holotype A.M. 8115
Stage of wear of teeth	(M+)	(W‡)	(M)	(M)	(W‡+)	(W+)	(W+)	(W‡)
Length (incl. supraoccipital crest and incisors)	(100)	(104)	112	116	—	((125))	((125))	((135))
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	(90)	(95)	101	103	—	((107))	((111))	(125)
Width (max.)	(60)	80	(90)	82	((85))	90	(96)	93.5
Width of brain case (max.)	34	36	34	38	—	39	(40)	44
Width, interorbital (min.)	30	33	36	35	—	43	39	46.5
Distance from anterior rim of orbit to anterior base of C/	36	36	48	40	(46)	42	44	43
Distance from anterior rim of orbit to supraoccipital crest	(70)	78	77	81	—	((87))	90	95
Width of muzzle at infra-orbital foramina	28.5	31	31	30	38	39	38	(40)
Width across canines	(20)	(19.5)	(22)	18.5	(23.5)	22	—	((19))
Length, C/–M^3 incl.	(52)	56	61.5	59	63	63.5	—	60.5
Length, P^1–M^3 incl.	(46)	50	54	52	54.5	54.5	57	54.5
Length, P^1–P^4 incl.	(21.5)	52	21.5	21.5	23	23.5	25.5	25
Length, M^1–M^3 incl.	28	29	33.5	31.5	31	33.5	35	31.5
Width of M^3 (max.)	10	10.5	13.5	14	11.5	12.5	10.5	13.5
Depth of malar below orbit	14	15.5	16.5	15	20	19.5	(23)	23

TABLE 12—(*Continued*)

	L. harveyi, new species	*L. decora* Leidy	*L. martini*, new species		*L. parasimus*, new species	*L. margeryae*, new species	*C. simus* Cope	*C. emydinus* Cope
MANDIBULAR RAMUS	Holotype U.N.S.M. 28450	Referred F:A.M. 45502	Holotype F:A.M. 45571A	Referred F:A.M. 45571B	Referred F:A.M. 45639	Holotype F:A.M. 45632	Referred A.M. 8117	Referred F:A.M. 56960
Stage of wear of teeth . . .					(M+)		(W)	(W+)
Length (max., incl. incisors) .	—	(97.3)	—	104	—	—	—	—
Length, /C-condyle incl. . .	—	89	—	90	—	—	—	—
Depth of jaw below anterior edge of M_3	21	22.5	—	23	27	26	22	29.5
Length, /C–M_3 incl.	—	58	—	60	66	—	64	(64.5)
Length, P_1–M_3 incl.	(49)	(52.5)	—	55.5	60.5	59	58	(58.5)
Length, P_1–P_4 incl.	(19)	20	—	20.5	24	22	21.5	(19.5)
Length, M_1–M_3 incl.	31	32.5	—	34.5	37	37.5	36.5	38

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] The only measurements of the lectotype of *L. decora* (A.N.S.P. 10878) are as follows: length, M^1–M^3 incl., 28 mm.; width of M^3 (max.), 10.5 mm.
[c] The holotype and referred specimens were found associated in the field. The holotype may represent a female and the referred a male.

ties, South Dakota; Dawes, Sioux, Scotts Bluff, Morrill and Garden counties, Nebraska; and Goshen County, Wyoming. ("Zone D" of Brule Formation.)

HOLOTYPE: Partial right maxilla, A.N.S.P. 10878. Figures 33, 38.

3. *Leptauchenia martini,* new species, from Morrill County, Nebraska; referred remains from Morrill, Sioux, Sheridan, and Scotts Bluff counties, Nebraska; and Shannon County, South Dakota. (Lower part of Gering Formation or deposits equal in age.)

HOLOTYPE: Skull and partial mandible, F:A.M. 45571A. Figures 33, 38, 40.

4. *Leptauchenia parasimus,* new species, from Niobrara County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; and Sioux, Sheridan, and Banner counties, Nebraska. (Upper part of Gering.)

HOLOTYPE: Partial skull, F:A.M. 34485. Figures 33, 38.

5. *Leptauchenia margeryae,* new species, from Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; and Morrill County, Nebraska. (Monroe Creek Formation.)

HOLOTYPE: Skull and mandible, F:A.M. 45632. Figures 33, 38, 40, 53.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

LEPTAUCHENIA

TOTAL AVAILABLE SPECIMENS: 231[1]

1. **Leptauchenia harveyi,**[2] new species

From oreodont faunal "Zone C" of the Brule Formation, Sioux County, Nebraska; referred remains from Shannon County, South Dakota

DESCRIPTION

SKULL: Smallest known of genus, approximate size of that of *Pseudocyclopidius orellaensis* from "Zone A"; mesocephalic; sagittal crest less prominent than in examples of *Leptauchenia decora;* frontals slightly reduced anteriorly, less so than in *L. decora;* infraorbital foramen above anterior portion of P^3; malar moderately deep, less so than in *L. decora;* bulla large for size of skull, as large as larger specimens of *L. decora.*

MANDIBLE: Light; moderately shallow; postsymphysis below anterior edge of P_3; ascending ramus high for size of skull.

DENTITION: Series shorter in length than in examples of *L. decora;* external style of superior molars prominent; individual teeth of series narrower in the lateral dimension than those of *L. decora.*

LIMBS: (Unknown).

[1] Includes 86 F:A.M. and 96 U.N.S.M. specimens.
[2] Named in honor of Cyril Harvey, member of U.N.S.M. field party, 1951–1955.

MEASUREMENTS: Table 12 (p. 274).

ILLUSTRATIONS: Figures 33, 38, 40.

DISCUSSION

Remains of *Leptauchenia harveyi* from oreodont faunal "Zone C" of the Brule Formation are the first of the leptauchenins occurring below "Zone D" ("*Leptauchenia*" beds) to be discussed in this report. Previously no examples of leptauchenins had been identified from below "Zone D." There are now three examples from "Zone C," and two (*Pseudocyclopidius orellaensis*) from "Zone A" of the Brule. These lower forms are rare and should shed light on the possibly ancestral form of the subfamily. The skulls from Brule "Zone C" are smaller than those from "Zone D" in their respective lines. The nasal-facial vacuities, however, are well established, and they are typical leptauchenins. One might hope that such early forms would reveal suggestive characters that would show more clearly the early phylogeny of the leptauchenins. No such characters, however, are apparent.

The overlapping of the external style of M^3 over the posterior edge of M^2 is not so pronounced as in examples of *L. decora.* In this respect, the holotype is similar to examples of *Sespia.*

The U.N.S.M. material was collected by C. Bertrand Schultz and associates, 1936, 1938, 1940, 1943; and one F:A.M. specimen, by Morris F. Skinner and associates, 1952.

Six specimens are here recorded:

HOLOTYPE

Skull with C/–P^1 rt. and P^2–M^3, and mandible with /C–P_1 rt. and P_2–M_3. (M+)	U.N.S.M. 28450	From oreodont faunal "Zone C" of Brule Formation, "13′ above lower white zone, top of Orella," Cheyenne River drainage, Hat Creek Basin, U.N.S.M. Coll. Loc. SX–15, Sioux County, Nebraska; collected by Cyril Harvey, Lloyd G. Tanner, C. Bertrand Schultz, and associates, 1953. Figures 33, 38, 40

REFERRED FROM (A) TYPE LOCALITY, SIOUX COUNTY, NEBRASKA; AND (B) SHANNON COUNTY, SOUTH DAKOTA

A. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–12:

SKULL AND MANDIBLE, IMMATURE		U.N.S.M.
Partial skull with C/–dP^2–M^2 and partial mandible with P_1–dP_3(br.)–M_2.	(I)	28497

A′. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–21:

MAXILLA		U.N.S.M.
Partial right maxilla with M^1(br.)–M^3	(W)	28259

FROM U.N.S.M. COLL. LOC. SX–22:

2 MAXILLA		
Partial right maxilla with P^3–M^2 (M^1 br.)	(W)	28498
Partial left maxilla with M^1–M^2	(M+)	28271

(B) FROM WHITE RIVER DRAINAGE, 5 MILES NORTHWEST OF SLIM BUTTE, SHANNON COUNTY, SOUTH DAKOTA

MAXILLAE AND MANDIBLE, IMMATURE		
Left and right maxillae with P^1–P^2 alv. and P^3–M^3 and partial mandible with P_1–P_2 rt. and dP_3–M_2	(I)	F:A.M. 56778

2. **Leptauchenia decora** Leidy

From oreodont faunal "Zone D" of the Brule Formation, "Valley of the White River," South Dakota; referred remains from Jackson, Fall River, Pennington, Shannon, and Washabaugh counties, South Dakota; Dawes, Sioux, Scotts Bluff, Morrill, and Garden counties, Nebraska; and Goshen County, Wyoming

Leptauchenia decora LEIDY, 1856a, p. 88; 1869, p. 127, pl. 12, figs. 11, 12. GIEBEL, 1883, pl. 44. SINCLAIR (in part), 1910, p. 196, fig. 1. ABEL, 1914, p. 167, fig. 122; 1919, p. 807, fig. 608; 1920, p. 436, fig. 661. O'HARRA, 1920, p. 127, fig. 64. THORPE (in part), 1937, p. 235, pl. 48, fig. 2 (pl. 35 not this species). SCOTT (in part), 1940, fig. 134, pl. 74, figs. 2–4, pl. 75, figs. 1, 1a, 3–12, 15.

Cyclopidius (*Chelonocephalus*) *schucherti*: THORPE, 1921b, p. 415, figs. 5, 6; 1937, p. 256, figs. 183–185.

Cyclopidius schucherti (Thorpe): LOOMIS, 1925a, p. 248. THORPE, 1937, p. 256, figs. 183–185.

CHARACTERS

SKULL: Largest known of genus; sagittal crest moderately high posteriorly, more so than in examples of *L. harveyi;* frontals slightly reduced anteriorly in front of midline of orbit; orbit looks forward more than in last-mentioned species; molar moderately deep below orbit, more so than in examples of *L. harveyi;* infraorbital foramen in area above posterior portion of P^3; auditory bulla well inflated, comparatively smaller than in examples of *L. harveyi.*

MANDIBLE: Light, heavier than in examples of *L. harveyi;* postsymphysis below anterior portion of P_4.

DENTITION: Series longer than in examples of *L. harveyi;* premolars slightly less crowded than in mentioned species; individual teeth wider than in examples of *L. harveyi.*

LIMBS: More robust than those of *Sespia,* but considerably lighter than those of *Hadroleptauchenia* and *Pseudocyclopidius.*

MEASUREMENTS: Table 12 (p. 274).

ILLUSTRATIONS: Figures 33, 38, 40, 41, 43, 53.

DISCUSSION

Leidy's[1] new genus and species *Leptauchenia decora* was based on a series of specimens. He stated: ". . . there are several specimens from the valley of the White River, Nebraska [Nebraska Territory = South Dakota] consisting of fragments of upper and lower jaws with teeth, . . .

"One of the fragments contains the left superior true molars and the last premolar (A.N.S.P. 10891)."

In Leidy's table of measurements he wrote:

"Length of series of upper true molars . . . . 15½ lines [=32.86 mm.]"
"Anteroposterior diameter of second true molar . . . . 5 lines [=10.60 mm.]"

The measurements and description of the maxilla agree with the maxilla, A.N.S.P. 10878, that is here selected as the lectotype. Leidy[2] also figured this same maxilla in 1869. Sinclair[3] illustrated a composite skeleton and referred it to *Cyclopidius decora.* The skeleton is made up of several individuals: parts of P.U. 10753 and 10773 (here referred to *Hadroleptauchenia primitiva*); forefoot of P.U. 10770 (here referred to *L. decora*); and a partial hind foot "enlarged to scale," P.U. 10765, which Sinclair referred to *"Leptauchenia" nitida.* Scott[4] considered P.U. 10765 referable to *L. decora* as do the present writers.

O'Harra,[5] Thorpe,[6] and Scott[7] accepted Sinclair's composite skeleton as *L. decora.* Scott, however, figured and gave the measurement of P.U. 10765 under *L. decora.* Scott also referred U.S.N.M. 2074 (pl. 74, figs. 1–16) to *L. decora* (here listed under *Hadroleptauchenia primitiva*).

Leidy[8] illustrated a partial skull and mandible, A.N.S.P. 10940, and referred it to *L. decora.* The skull and mandible are now separated and shown to be an immature individual referable to *Pseudocyclopidius major* (p. 333). Thorpe,[9] who also considered this specimen as part of the genocotype of *L. decora,* stated: "Genocotypes and genoparatypes not differentiated. Cat. Nos. 10875-10940 A.N.S.P." The present writers list the A.N.S.P. specimens that could be found and considered referable to this species.

Loomis[10] reported: "Thorpe erected another genus under the name *Chelonocephalus* with *C. schucherti* as its type. This is an exaggerated *Cyclopidius,* and it is largely a question of personal judgment as to how much a species must deviate in order to require a separate genus. I should include this species with the others under *Cyclopidius.*"

The present writers fail to recognize characters of the type of *Chelonocephalus schucherti* that would differentiate it from other referred skulls of *L. decora.*

Thorpe gave the type locality of *"C. schucherti"* as "near Hermosa, South Dakota," and the geologic occurrence as "middle Miocene (Sheep Creek)."

It is pertinent that an example of *Paramerycoidodon (Barbourochoerus) major* (Leidy), Y.P.M. 12273 (p. 95), also from "Zone D" of the Brule, is documented as follows: collected by H. F. Wells, 1894, and "shipped from Hermosa," South Dakota.

The present writers and Morris F. Skinner visited the "Hermosa" area; they doubt that

[1] 1856a, p. 88.
[2] 1869a, pl. 12, figs. 11–12.
[3] 1910, fig. 1.
[4] 1940, p. 703, pl. 75, figs. 1–1a, 3–12, 13–15.
[5] 1920, fig. 64
[6] 1937, pl. 48, fig. 2.
[7] 1940, fig. 134.
[8] 1869, pl. 12, fig. 6.
[9] 1937, pp. 234–235.
[10] 1925a, p. 248.

there are deposits in that area equal in age to the Sheep Creek. Oligocene deposits, however, are not too far distant. No leptauchenins have been reported above the Monroe Creek Formation. Had the geologic range of the subfamily extended into the middle Miocene, it seems likely that the large collections from the Sheep-Snake Creek area would have included some indication of the group.

The F:A.M. specimens from South Dakota and Nebraska were collected by Morris F. Skinner and associates (Ralph Mefferd and Gordon Fletcher, 1938; Ralph Mefferd, 1939, 1940; Ove Kaisen and Morris F. Skinner, Jr., 1944; Ove Kaisen, Leonard Nelson, and Morris F. Skinner, Jr., 1945; Thomas Lucas and Morris F. Skinner, Jr., 1950; Robert E. Lamb, Morris F. Skinner, Jr., and Loren M. Toohey, 1951; Alan L. Lamb, Thomas Lucas, and Morris F. Skinner, Jr., 1953; Morris F. Skinner, Jr., and Loren M. Toohey, 1954; and Ted Galusha, Robert Emry, and Carl Elfgren, 1958). The U.N.S.M. collections were made from 1932 to 1940 and from 1950 to 1952. The earlier U.N.S.M. field parties included the following collectors: E. L. Blue, Frank W. Crabill, Frank R. Denton, Loren C. Eiseley, Gordon Graham, Robert Kubicek, Robert Long, John Mercer, Marian and Bertrand Schultz, Mylan Stout, S. R. Sweet, Lloyd G. Tanner, Harry Tourtelot, Eugene Vanderpool, and Lynn Robert Wolfe. The 1950 to 1952 parties included: Jerry Folsom, W. D. Frankforter, Cyril Harvey, Edward F. Sabatka, C. Bertrand Schultz, Lloyd G. Tanner, and Loren M. Toohey.

Two hundred and three specimens are here recorded:

LECTOTYPE

Partial right maxilla with P^4–M^3. (w)	A.N.S.P. 10878	From oreodont faunal "Zone D" of Brule Formation, "Valley of the White River," South Dakota; collected by F. V. Hayden in 1855 Figured by Leidy, 1869, pl. 12, figs. 11, 12 This report, figures 33, 38

REFERRED FROM (A) SOUTH DAKOTA; (B) JACKSON, (C) FALL RIVER, (D) PENNINGTON, (E) SHANNON, AND (F) WASHABAUGH COUNTIES, SOUTH DAKOTA; (G) DAWES, (H) SIOUX, (I) SCOTTS BLUFF, (J) MORRILL, AND (K) GARDEN COUNTIES, NEBRASKA; AND (L) GOSHEN COUNTY, WYOMING

A. FROM SOUTH DAKOTA (COLLECTED BY F. V. HAYDEN IN 1855)

FROM THE "VALLEY OF THE WHITE RIVER":

9 MAXILLAE

		A.N.S.P.
5 partial right maxillae with		
dP^3–M^2	(I)	10875
M^1–M^3	(w+)	10876
dP^4–M^1	(I)	10877
M^1(br.)–M^3	(w‡+)	10882
P^3–M^2 (P^3–P^4 erupt.)	(−M)	10884
4 left maxillae with		
dP^3–M^2	(I)	10879
M^1–M^3	(w‡)	10880
M^1–M^3	(w+)	10881
dP^4–M^2	(I)	10883

7 MANDIBULAR RAMI

4 partial right rami with		
M_1–M_3(germ)	(I)	10885
dP_3–M_2(br.) (M_1 br.)	(I)	10886
M_2–M_3	(w)	10887
M_1–M_2	(w)	10889

3 partial left rami with		A.N.S.P.
M_2(br.)–M_3	(w+)	10888
P_3–dP_4	(I)	10892
M_3	(M+)	10893

MANDIBULAR SYMPHYSIS

Partial symphysis with I_1–/C rt. and P_1–M_3	(w)	10891

B. FROM WHITE RIVER DRAINAGE, JACKSON COUNTY, SOUTH DAKOTA

FROM W. OF CEDAR PASS:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS, IMMATURE

Skull with C/–dP^2–M^3(germ) (P^1 rt.), and mandible with dP_2–M_3(germ), partial scapula, humerus, radius, ulna, ribs, and vertebrae. Figure 43	(I)	F:A.M. 45565

8 SKULLS AND MANDIBLES, ATTACHED

8 partial skulls and mandibles with		
C/–dP^2–M^2; /C–dP_2–M_2	(I)	45521
C/(br.)–dP^2–M^2; /C–dP_2–M_2	(I)	45524
P^3–M^3; M_3	(w‡)	45538
P^2–M^3; P_3–M_3	(w‡)	45539
P^3–M^3; P_4–M_3	(w)	45542
I^3–M^3; I_3–M_3	(w)	45561
		U.N.S.M.
P^4–M^3; P_3–P_4 rt. and M_1–M_2 (left ramus only)	(M+)	28404
P^4–M^3; P_4–M_3	(w)	28499

3 MAXILLAE

Partial right and left maxillae with P^2 and M^1(br.)–M^2	(M+)	28516
Partial left maxilla with M^1(br.)–M^3	(w)	28403

FROM E. OF CEDAR PASS:

SKULL, MANDIBLE, AND HUMERUS

		F:A.M.
Partial skull with P^3–M^3, partial mandible with P_2–M_3, and partial humerus	(M)	45550

15 PARTIAL SKULLS AND MANDIBLES

15 partial skulls and mandibles with		
P^1(rt.)–dP^2–M^2; I_1–P_1 rt. and dP_2–M_2	(I)	45522
dP^2–M^2; P_1–dP_2–M_2	(I)	45527
C/–M^3; I_1(rt.)–M_3 (attached)	(w‡)	45541
M^2(br.)–M^3; M_3 (attached)	(w)	45543
P^2–M^3; P_3–M_3 (right ramus only)	(w)	45544
P^2–M^3 br.; P_4–M_3 (attached)	(w‡+)	45545
M^1–M^3; M_2(br.)–M_3 (attached)	(w)	45547
P^3–M^3; M_1–M_3	(w+)	45551
P^2–M^3; P_2(br.)–M_3	(w)	45557
C/–M^3 (M^1 br.); P_1–M_3	(w+)	45559
P^4–M^3; P_2(rt.)–M_3	(M)	45560
P^1–dP^2–M^2(br.); P_1–dP_2–M_2 (M_1 absent)	(I)	45562
C/–M^3; I_1–M_3	(M)	45564
C/(rt.)–M^3 (P^1 br.); P_1–M_3	(w)	45640
P^2–M^3; P_2–M_3 (M_1 br.)	(w)	56779

7 PARTIAL SKULLS

7 partial skulls with		
C/–P^4 rt. and M^1–M^3	(w+)	45540
C/–P^3 rt. and P^4–M^3	(M)	45546

		F:A.M.
$C/-M^3$	(W+)	45548
P^3-M^3	(M+)	45549
$C/-M^3$ (P^2-P^4 and M^3 erupt.)	(−M)	45552
C/(rt.)–M^3	(W)	45553
dP^3-M^2	(I)	45563

C. FROM WHITE RIVER DRAINAGE, FALL RIVER COUNTY, SOUTH DAKOTA

FROM 7 MI. NW. OF SLIM BUTTE:

6 SKULLS AND MANDIBULAR RAMI		F:A.M.
Partial skull with P^1(rt.)–M^3 and mandible (attached) with P_1-M_3	(W)	56781
Partial skull with M^2(br.)–M^3 and mandible (attached) with M_2-M_3	(W)	56782
Partial skull with I^3-M^3 (C/ br., P^2 alv.) and partial mandible (attached) with P_1-M_2 (P_2-M_1 br.)	(W+)	56783
Partial skull with P^2-M^3 and mandible (attached) with I_1-P_2 rt. and P_3-M_3	(M+)	56784
Partial skull with P^2(rt.)–M^3 and mandible (attached) with I_2-P_1 rt. and P_2-M_3	(W)	56785
Partial skull with P^1(br.)–M^3 (P^2 rt.) and right ramus with P_1-M_3(br.) (P_2 rt.)	(M+)	56786

SKULL		
Partial skull with C/(br.)–M^3 (P^2 rt. and P^3 br.)	(W‡)	56787

FROM LITTLE BAD LANDS, NEAR OELRICHS (COLLECTED BY F. B. VAN HOUTEN):

SKULL AND MANDIBLE		P.U.
Skull with dP^2-M^2 and mandible (left ramus attached) with P_2(br.)–dP_3-M_2. Figured by Scott, 1940, pl. 74, figs. 3–4	(I)	14548

It is possible that the above specimen is referable to *Hadroleptauchenia*.

D. FROM WHITE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

FROM N. SIDE OF PINNACLES:

3 SKULLS AND MANDIBLES		F:A.M.
Partial skull with dP^3-M^2 and mandible with dP_4-M_2	(I)	45526
Partial skull with P^1(br.)–M^3 and mandible with P_1(br.)–M_3	(M)	56788
Skull with $C/-M^3$ and mandible with P_1-M_3	(W+)	56789

D′. FROM FIRST CANYON NORTH OF SCHOOL OF MINES CANYON, CHEYENNE RIVER DRAINAGE, PENNINGTON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE (ATTACHED)		F:A.M.
Skull with P^1(br.)–M^3 and mandible with $/C-M_3$ (P_1 br.)	(W)	56790

FROM "NEAR HERMOSA" (COLLECTED BY H. F. WELLS, 1894);

SKULL		Y.P.M.
Skull with $C/-P^1$ br. and P^2-M^3	(W)	10123

The above skull is the holotype of "*Cyclopidius* (*Chelonocephalus*) *schucherti*" of Thorpe. The type locality was given as "near Hermosa, South Dakota," and the geologic horizon as "Middle Miocene (Sheep Creek)." The Hermosa area has been visited by the present writers and Morris F. Skinner. No deposits were recognized that could be attributed to Sheep Creek age. The specimen is a typical example of *Leptauchenia decora* from the upper Oligocene deposits of South Dakota and Nebraska. (See discussion, p. 278.)

E. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM COTTONWOOD CREEK AREA (COLLECTED BY J. B. HATCHER, 1893 AND 1897):

2 ASSOCIATED SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS		P.U.
Skull with C/(br.)–M^3, mandible with P_1–M_3, and atlas (all attached)	(W)	10765
Partial skull with C/(br.)–M^3(P^1 rt.), partial left ramus with P_4–M_3 (br.)	(W)	10765
3 partial scapulae, humerus, 2 partial pelvi, 2 calcanea, 2 astragali, vertebrae, and ribs; smaller sized individual with 2 femora, partial tibia, partial fibula, partial pes; larger sized individual with femur, 2 tibiae, fibula, and partial pes		10765

The above two partial skeletons were figured by Scott, 1940, pl. 75, figs. 1–1a, 2–12, 13–15. The explanation of the plates stated, " . . . from two associated skeletons." Sinclair[1] considered the above material referable to "*Cyclopidius nitida*" (=*Sespia nitida*).

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with I^2–M^3, mandible (attached) with I_1–M_3, 2 partial humeri, partial radius, 2 femora (1 partial), 2 partial tibiae, partial pelvis, various metapodials, and fragments. Femur (only) figured by Scott, 1940, pl. 75, fig. 12a; Sinclair, 1910, fig. 1 (in part)	(W+)	10770

FROM $\frac{3}{4}$–$1\frac{1}{4}$ MI. S. OF COTTONWOOD PASS:

5 SKULLS AND MANDIBLES		F:A.M.
5 partial skulls and mandibles with		
C/(br.)–M^3; I_1–I_3 alv. and /C(rt.)–M_2	(M+)	45505
C/–P^1 rt. and P^2–M^3; I_1–/C rt. and P_1–M_3	(W+)	45506
P^2–M^3; P_1(br.)–M_3	(W)	45507
C/–M^3; /C–M_3	(W+)	45509
dP^1–M^2; I_2–/C rt. and P_1–dP_2(rt.)–M_2	(I)	45525

3 SKULLS		
Partial skull with C/–M^3	(W+)	45504
Partial skull with M^1(br.)–M^3	(M+)	45510
Partial skull with P^3–M^3. Figure 53 (in part)	(M)	45503

FROM HEAD OF E. FORK OF BIG CORRAL DRAW:

3 SKULLS AND MANDIBLES (ATTACHED)		
Partial skull with dP^1–M^2 and mandible with dP_3–M_2	(I)	45519
Skull with P^1–P^4 br. and M^1–M^3 and mandible with P_1–M_3	(W$\ddagger^{+}$)	45520
Partial skull with C/–M^3 and mandible with P_1–M_3	(M+)	56791

FROM AREA BETWEEN HEADS OF BIG CORRAL DRAW AND COTTONWOOD CREEK:

3 SKULLS AND MANDIBLES (ATTACHED)		
Skull with I^3–M^3 and mandible with I_1–M_3	(W)	45508
Skull with C/(br.)–M^3 and mandible with P_2(br.)–M_3	(W+)	45511
Partial skull with I^3–dP^2–M^2 and mandible with I_1–dP_2–M_2(br.)	(I)	45512

SKULL		
Partial skull with C/(br.)–dP^2–M^2	(I)	45515

FROM CORRAL DRAW (COLLECTED BY J. B. HATCHER, 1893):

[1] 1910, p. 196.

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with C/(br.)–M^3, mandible (attached) with /C(rt.)–M_3, 2 humeri, 2 radii (1 partial), partial tibia, 2 calcanea, astragalus, partial pes, and fragments. Figured by Sinclair, 1910, fig.1 (in part); Thorpe, 1937, pl. 48, fig. 2 (in part)	(w)	P.U. 10773
Partial skull with P^3–M^3, mandible (attached) with P_3–M_3, and atlas. Figured by Scott, 1940, pl. 74, figs. 2–2a. (If P. U. 10756 is the illustrated specimen, considerable restoration is present in the drawing.)	(M+)	10756

FROM SW. SIDE OF SHEEP MT.:

SKULL AND MANDIBLE

Partial skull with C/–P^2 br. and P^3–M^3 (M^1 br.) and partial mandible with P_1(br.)–M_3	(w‡+)	F:A.M. 56792

SKULL

Partial skull with P^1(rt.)–M^3	(w+)	56793

E′. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM E. SIDE OF SHEEP MT.:

SKULL AND MANDIBLE (ATTACHED), IMMATURE

Partial skull with dP^2–M^2 and mandible with P_1–dP_2–M_2	(I)	F:A.M. 56794

FROM 5 MI. NW. OF SLIM BUTTE:

SKULL

Skull with P^1(rt.)–M^3	(w)	45569

F. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM HAY CREEK AREA:

SKULL, MANDIBLE (ATTACHED), AND SKELETAL ELEMENTS

Partial skull with P^2–M^3, mandible with I_1–I_2 rt. and I_3–M_3, 2 partial scapulae, 2 humeri, 2 partial radii, 2 partial ulnae, and ribs	(w‡+)	F:A.M. 45582

SKULL AND MANDIBLE

Skull with C/(br.)–M^3 and mandible with I_1–I_3 alv. and /C–M_3 (P_1 rt.). Figures 33, 38, 40, 41	(w)	45502

8 SKULLS AND MANDIBLES (ATTACHED)

8 partial skulls and mandibles with

C/(alv.)–M^3 (P^1 alv.); /C(rt.)–M_3	(w)	45570
C/(rt.)–P^1–dP^2–M^2; P_1(rt.)–dP_2–M_2	(I)	45583
dP^3–M^2; dP_3–dP_4(br.)–M_2	(I)	45587
dP^2–M^1; dP_3–M_1	(I)	45590
M^1(br.)–M^3; /C–P_2 rt. and P_3–M_3 (P_4 br.)	(w‡)	45591
I^3–M^3; I_3–M_3	(w)	45593
C/(rt.)–dP^2–M^2; P_1–dP_2 br. and dP_3–M_2	(I)	45594
dP^2–M^2(erupt.); I_2–I_3 alv. and /C(rt.)–dP_3–M_2 (erupt.) (P_1 br.)	(I)	45595

FROM 8–9 MI. S. AND 2 MI. W. OF INTERIOR, HAY CREEK:

4 SKULLS AND MANDIBLES

Partial skull with P^1–M^3 and mandible (attached) with P_1(rt.)–M_3	(M+)	45586
Partial skull with C/(rt.)–M^3 and mandible with /C(rt.)–M_3	(w+)	45588
Partial skull with P^2–M^3 and mandible with I_1–P_1 rt. and P_2–P_3	(w+)	45592
Partial skull with I^3–dP^2–M^3 and mandible with P_1–dP_2–M_2	(I)	56797

2 SKULLS AND MANDIBLES (ATTACHED)		F:A.M.
2 partial skulls and mandibles with		
P^1(rt.)–M^3; P_1(rt.)–M_3	(M)	45589
P^3–M^3; P_3–M_3	(M)	45596

2 SKULLS		
2 partial skulls with		
dP^2–M^2	(I)	45523
P^3–M^3	(W+)	45584

G. FROM WHITE RIVER DRAINAGE, $\frac{1}{4}$ MILE SOUTHWEST OF CHADRON STATE TEACHERS COLLEGE CAMPUS, CHADRON, DAWES COUNTY, NEBRASKA

SKULL AND MANDIBLE (ATTACHED)		U.N.S.M.
Skull with I^1–dP^2–M^2 and mandible with I_2–I_3 rt. and /C–dP_3–M_2	(I)	28185

H. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM THE AREA OF U.N.S.M. COLL. LOC. SX–17 AND 19:

9 ASSOCIATED INDIVIDUALS

3 MAXILLAE		U.N.S.M.
Partial right maxilla with P^2–M^2	(W‡)	28454A
Partial left maxilla with I^2–P^1 rt. and P^2(br.)–M^3	(W‡)	28454B
Partial left maxilla with P^3(br.)–M^3	(W‡)	28454C

6 MANDIBULAR RAMI		
3 right rami with		
P_1–P_2 br. and P_3–M_3	(W+)	28454D
P_4(br.)–M_3	(W‡)	28454E
I_1–P_3 rt. and dP_4–M_1	(I)	28454F
3 left rami with		
P_3(rt.)–M_3	(W)	28454G
P_1(rt.)–M_2	(W)	28454H
P_4(rt.)–M_3	(W‡)	28454I

FROM U.N.S.M. COLL. LOC. SX–20:

MANDIBLE		
Partial mandible with P_3–M_3	(M+)	28517

FROM THE AREA OF U.N.S.M. COLL. LOC. SX–20 AND 21:

SKULL		
Skull with P^1(rt.)–M^3	(M+)	28430

MAXILLA		
Partial left maxilla with P^3–M^3	(W+)	28518

FROM U.N.S.M. COLL. LOC. SX–21:

3 SKULLS AND MANDIBULAR RAMI		
Skull with P^1(rt.)–M^3 and mandible with /C–M_3 (P_1–P_2 rt.)	(W+)	28224
Partial skull with P^1–M^3 and left ramus with P_1(rt.)–M_3 (P_3 rt.)	(M+)	28519
Skull with I^2–dP^2–M^2 and mandible (attached) with I_1–dP_2–M_2	(I)	28520

MAXILLA		
Partial left maxilla with M^1(br.)–M^3	(W+)	28270

3 MANDIBULAR RAMI		U.N.S.M.
Partial right ramus with P_1(alv.)–M_3	(w‡)	28211
Partial left ramus with M_1–M_3	(w)	28221
Partial mandible with P_3–P_4 rt. and M_1–M_3(br.)	(w)	28266

FROM U.N.S.M. COLL. LOC. SX–22:

2 ASSOCIATED INDIVIDUALS		
Partial skull with dP^3–M^2(br.) and partial left ramus with M_1–M_2	(I)	28429A
Partial right ramus with P_1(alv.)–M_3	(w+)	28429B

The above two specimens were found associated in the field.

2 ASSOCIATED INDIVIDUALS		
Partial skull with P^2–M^3 and partial mandible (attached) with P_1–M_3	(w)	28521A
Partial right ramus with P_2–M_2(erupt.) (P_3–P_4 rt.)	(I)	28521B

The above two individuals were found associated in the field.

5 SKULLS AND MANDIBULAR RAMI		
Partial skull with M^1–M^3 and partial right ramus with M_1–M_3	(–M)	28424
Fragmentary skull with dP^3–M^3(erupt.) and mandible with /C–P_1 rt. and dP_3–M_3 (erupt.)	(I)	28522
Skull with C/–dP^2–M^2 and mandible (attached) with /C(rt.)–dP_2–M_2	(I)	28523
Partial skull with dP^2–M^2 and partial mandible with dP_2–M_2	(I)	28524
Skull with C/–dP^2–M^2 and mandible (attached) with /C(rt.)–dP_2–M_2	(I)	28525

2 MAXILLAE AND MANDIBULAR RAMI		
Partial left maxilla with P^4–M^3 and partial mandible with P_3–M_3	(M)	28265
Partial left maxilla with P^4–M^3 and partial right ramus with P_1–P_3 rt. and P_4–M_3	(M)	28526

SKULL		
Skull with C/(br.)–dP^2–M^2	(I)	28183

MAXILLA		
Partial right maxilla with P^4–M^3	(M)	28527

FROM U.N.S.M. COLL. LOC. SX-27:

SKULL AND MANDIBLE		
Partial skull with P^4–M^3 and mandible (attached) with P_4–M_3	(w)	28457

SKULL		
Partial skull with P^2–M^3	(w)	28528

FROM U.N.S.M. COLL. LOC. SX–43:

MAXILLA		
Partial right maxilla with P^4–M^3(br.)	(M)	28529

H′. FROM NORTH PLATTE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM 13½ MI. N. OF SCOTTSBLUFF:

SKULL AND MANDIBLE		U.N.S.M.
Fragments of skull with P^1–M^3 and mandible with P_2(alv.)–M_3	(M+)	28256

SKULL		
Partial skull with C/(br.)–M^3 (P^1 rt.)	(M+)	28428

FROM BLACKBURN RANCH, N. OF MITCHELL, "LOWER ASH" OF WHITNEY:

SKULL, MANDIBULAR RAMUS, AND SKELETAL ELEMENTS

Partial skull with M^1–M^3, partial right ramus with M_1–M_2, partial humerus, partial radius, 2 partial ulna, and vertebrae	(M)	F:A.M. 56798

I. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM ROUND TOP, N. SIDE OF WILDCAT RIDGE:

SKULL AND MANDIBULAR RAMUS

		U.N.S.M.
Partial skull with M^1–M^3 and partial right ramus with M_1(br.)–M_3	(M+)	28530

SKULL

Skull with P^1(rt.)–M^3 (P^2 br.)	(W)	28531

FROM ROUBIDEAUX PASS, N. SIDE OF WILDCAT RIDGE:

MANDIBLE

Partial mandible with M_1–M_3	(W+)	28532

J. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM BRIDGEPORT AREA:

2 SKULLS AND MANDIBLES

		U.N.S.M.
Anterior portion of skull with C/–M^2 and partial mandible (attached) with P_1–M_2	(W‡‡)	28434
Anterior portion of skull with P^2–M^3 and partial mandible with P_4–M_3	(W+)	28609

2 MAXILLAE

Partial right maxilla with P^2–M^2	(W)	28435
Partial right maxilla with P^4–M^3	(–M)	28533

MANDIBLE

Partial mandible with I_3–P_2 rt. and P_3–M_3	(W+)	28237

4 MANDIBULAR RAMI

Partial left ramus with P_3(rt.)–dP_4–M_2(germ)	(I)	28414
Partial right ramus with dP_3–M_1	(I)	28534
Partial right ramus with P_1–P_2 alv. and P_3–M_3	(W+)	28535
Partial right ramus with M_1–M_3	(M+)	28536

FROM U.N.S.M. COLL. LOC. MO–101:

MANDIBULAR RAMUS

Right ramus with I_3–/C alv. and P_1–M_3	(W‡)	28537

FROM U.N.S.M. COLL. LOC. MO–109:

SKULL

Inferior portion of skull with dP^2–M^2	(I)	28538

FROM U.N.S.M. COLL. LOC. MO–111:

SKULL AND MANDIBLE

Partial skull with I^2–M^3 (P^1 br.) and partial mandible with I_2–M_3	(W‡)	28207

3 SKULLS

Partial skull with P^1–M^3	(M+)	28426
Partial skull with P^3–M^3	(W)	28539
Partial skull with C/–M^3	(W)	28540

MAXILLA		U.N.S.M.
Partial left maxilla with C/(rt.)–M^3	(w‡)	28238
3 MANDIBULAR RAMI		
Partial right ramus with P_1–P_2 alv. and P_3–M_3	(w+)	28541
Partial right ramus with P_1–M_3	(w)	28542
Partial right ramus with P_1(erupt.)–dP_3–M_1	(i)	28251

FROM U.N.S.M. COLL. LOC. MO–112 (=F:A.M. COLL. LOC. "5 MI. E. BROADWATER"):

3 ASSOCIATED INDIVIDUALS, IMMATURE		
Partial left maxilla with dP^2–M^1 and partial mandible with I_1–dP_3–M_1 (P_1 alv.)	(i)	28543A
Left portion of skull with I^3–C/ erupt. and P^1(rt.)–dP^2–M^1	(i)	28543B
Partial right ramus with I_1–dP_3–M_1 (P_1 alv.)	(i)	28543C
Partial right ramus with dP_4–M_1	(i)	28543D
Left M_1	(i)	28543E
Left dP_4	(i)	28543F
3 SKULLS AND MANDIBLES (ATTACHED)		
3 partial skulls and mandibles with		
I^3–M^3; P_1–M_3.	(w‡)	28425
P^1–dP^2–M^2; I_1–dP_3–M_2	(i)	28544
		F:A.M.
dP^2–M^1; dP_3–M_1	(i)	56799
SKULL		
Partial skull with P^1–dP^2–M^2	(i)	56800
2 MANDIBLES		
Partial mandible with P_1–P_2 rt. and P_3–M_3	(w+)	28545
Partial mandible with M_2–M_3	(m+)	28546

J′. FROM PUMPKIN CREEK VALLEY, NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM S. OF BRIDGEPORT:

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with I_3–/C rt. and P_1(br.)–M_3	(w)	28267

FROM U.N.S.M. COLL. LOC. MO–104:

SKULL AND MANDIBLE		
Partial skull with C/–M^2 and partial mandible with I_1–I_3 alv. and /C–M_1(br.)	(i)	28215
4 MANDIBULAR RAMI		
Mandible with I_2–M_3	(w+)	28218
3 partial right rami with		
P_2–dP_3–M_2	(i)	28418
I_1–/C alv. and P_1–dP_3–dP_4	(i)	28419
M_1–M_2	(−m)	28423

FROM U.N.S.M. COLL. LOC. MO–106:

SKULL AND MANDIBLE, IMMATURE		
Partial skull with C/(rt.) P^1–dP^2–M^2(br.) and partial mandible with P_1–P_2 rt. and P_3–M_1	(i)	28547

FROM U.N.S.M. COLL. LOC. MO–107:

2 SKULLS AND MANDIBLES		U.N.S.M.
Parts of skull with $C/–M^3$ and partial mandible with P_1(br.)–M_3	(W+)	28258
Left and right maxilla with $C/–M^3$ (M^1 br.) and partial mandible with $I_1–I_3$ rt. and $/C–M_3$ (P_1 rt.)	(W‡)	28437
2 SKULLS		
Partial skull with P^1(rt.)–M^3 (M^1 br.)	(W+)	28255
Left and right maxillae with P^1(alv.)–M^3	(M+)	28436
MAXILLA AND MANDIBLE		
Left maxilla with $C/–M^3$ and partial mandible with P_1(br.)–M_3 (P_2 br.)	(W)	28548
3 MAXILLAE		
Partial right maxilla with $C/–M^3$ (P^1 and P^4 alv.)	(W+)	28549
Partial right maxilla with P^1(rt.)–M^3	(W‡)	28550
Partial left maxilla with P^1–dP^2(alv.)–M^2	(I)	28433

K. FROM NORTH PLATTE RIVER DRAINAGE, NEAR LEWELLEN, GARDEN COUNTY, NEBRASKA (COLLECTED BY T. M. STOUT, 1931)

MAXILLA		U.N.S.M.
Partial right maxilla with $C/$(br.)–M^3	(W)	28551
MANDIBULAR RAMUS		
Partial left ramus with I_3–dP_2–M_2 br.	(I)	28552

L. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK AREA, NORTH SIDE OF 66 MOUNTAIN, GOSHEN COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		F:A.M.
Skull with $C/–M^3$, mandible with $P_1–M_3$, (P_2 alv., $P_3–P_4$ br.), 2 humeri (1 partial), partial ulna, and radius	(W‡)	57139

3. **Leptauchenia martini**,[1] new species

From deposits equal in age to the lower part of Gering Formation, Washabaugh County, South Dakota; referred remains from Washabaugh, Jackson, and Shannon counties, South Dakota; and from the lower Gering, Sheridan, Sioux, Scotts Bluff, and Morrill counties, Nebraska

DESCRIPTION

SKULL: Small in size; within size range of that of *Leptauchenia decora* (from "Zone D" of Brule), smaller than in examples of *L. parasimus* (from upper part of Gering); narrower than in latter species; tendency to be more depressed than in *L. decora,* similar to *L. margeryae* in this respect; frontal with less invasion of nasal-facial vacuity than in latter species, similar to examples of *L. decora* in this respect.

MANDIBLE: Less robust than in examples of *L. margeryae;* more as in those of *L. parasimus;* symphysis with less depth than in other examples of genus, more as in those of *L. decora.*

DENTITION: Over-all length close to that of *L. decora;* slightly more hypsodont than in that species, more as in *L. parasimus* and *L. margeryae* in this respect; premolars slightly larger than in *L. decora.*

LIMBS: (Unknown).

MEASUREMENTS: Table 12 (p. 274).

ILLUSTRATIONS: Figures 33, 38, 40.

DISCUSSION

The skulls of *Leptauchenia martini* from the lower Gering Formation are smaller than those

[1] Named in honor of Donald Martin, a preparator at the University of Nebraska State Museum, who has aided in the preparation of the oreodont specimens.

from the upper Gering (*L. parasimus*) and from the Monroe Creek Formation (*L. margeryae*), but are only slightly larger than examples of *L. decora* from "Zone D" of Brule.

The dentition of *L. martini* is more hypsodont than that of *L. decora*. There was a tendency among the leptauchenins in general for the dentitions to become more hypsodont during the Miocene and it is evident in all of the six independent phylogenetic lines.

The F:A.M specimens were collected by Morris Skinner and associates, 1938–1960; and the U.N.S.M. examples, by E. L. Blue, Thompson M. Stout, Marian Schultz, Bertrand Schultz, and associates, 1931–1941.

Twenty-seven specimens are here recorded:

HOLOTYPE

Skull with I^3–M^3. (M) F:A.M. 45571A From Gering Formation equivalent, "35′ above lower white ashy layer (=first white layer)," E. side Potato Creek, W. of Whitney White's Ranch, White River drainage, Washabaugh County, South Dakota; collected by Morris Skinner, Ralph Mefferd, and associates

Figures 33, 38

The skull (holotype) is heavier and wider than the associated specimen, F:A.M. 45571B, listed below, and probably represents a male. The lighter and narrower associated specimen may represent a female. The present writers chose F:A.M. 45571A as the holotype, since it was more typical of the species.

ASSOCIATED WITH HOLOTYPE

SKULL AND MANDIBLE		F:A.M.
Skull with I^2(rt.)–M^3 and mandible with I_1–M_2. Figures 33, 40	(M)	45571B

REFERRED FROM (A) WASHABAUGH, (B) JACKSON, AND (C) SHANNON COUNTIES, SOUTH DAKOTA; AND (D) SHERIDAN, (E) SIOUX, (F) SCOTTS BLUFF, AND (G) MORRILL COUNTIES, NEBRASKA

A. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM 18 MI. S. OF KADOKA:

SKULL		F:A.M.
Partial skull with P^1–M^3	(W‡)	45567

FROM W. SIDE OF PASS CREEK:

SKULL		
Partial skull with C/(br.)–M^3 (P^1 alv.).	(M+)	56858

FROM 8 MI. S. AND 2 MI. W. OF INTERIOR:

SKULL AND MANDIBLE		
Partial skull with P^2–M^3 and partial mandible with P_2–P_3 alv. and P_4–M_3	(M+)	56796

FROM 5 MI. NW. OF WANBLEE:

SKULL		
Partial skull with M^1(br.)–M^3	(W)	45578

FROM E. SIDE OF POTATO CREEK:

SKULL		
Fragmentary skull with P^3(br.)–M^3 and mandible with P_3 (alv.)–M_3	(W‡)	45575

B. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA, JACKSON COUNTY, SOUTH DAKOTA

FROM 20′ ABOVE WHITE LAYER, TOP OF CEDAR PASS:

SKULL		F:A.M.
Inferior portion of skull with P^4–M^3	(M+)	56780

FROM E. OF CEDAR PASS:

2 SKULLS AND MANDIBLES		
Skull with C/–dP^2–M^2 and mandible with I_2–dP_2–M_2	(I)	45529
Skull with C/(br.)–dP^2–M^2 and mandible with P_1–dP_2–M_2(br.)	(I)	45536

FROM ¼–1 MI. E. OF CEDAR PASS:

2 SKULLS AND RAMI		
Partial skull with dP^2–M^2 and partial right ramus with dP_4–M_2	(I)	45641
Fragmentary skull with C/–dP^2–M^2 (P^1 alv.) and mandible with P_1–dP_2–M_2 (P_3–P_4 absent)	(I)	45531

The above specimen is tentatively referred to this species.

FROM 1 MI. NE. OF CEDAR PASS:

2 SKULLS AND MANDIBLES		
Partial skull with P^3–M^3 (M^1 br.) and partial mandible (attached) with P_4–M_3	(W+)	56859
Partial skull with C/–M^3 and partial mandible with P_4–M_1 br. and M_2–M_3	(W+)	45574

C. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM 7 MI. BELOW [=N. OF] PORCUPINE:

MANDIBULAR RAMUS		F:A.M.
Partial left ramus with P_3(br.)–M_3	(W)	37230

FROM 7 MI. E. OF ROCKYFORD:

SKULL AND MANDIBLE (ATTACHED)		
Partial skull with C/–M^3 and mandible with I_1–/C rt. and P_1–M_3	(W)	56861

D. FROM WHITE RIVER DRAINAGE, PINE RIDGE AREA, NORTH OF RUSHVILLE, SHERIDAN COUNTY, NEBRASKA

MAXILLA		U.N.S.M.
Partial left maxilla with M^1–M^2 alv. and M^3	(W‡‡)	28555

E. FROM WHITE RIVER DRAINAGE, PINE RIDGE AREA, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–22:

MAXILLA		U.N.S.M.
Partial right maxilla with C/(rt.)–M^2(br.) (P^1 and M^1 br.)	(W+)	28554

E′. FROM NORTH PLATTE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM 13½ MI. N. OF SCOTTS BLUFF:

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with I_1–I_3 alv. and /C–P_1–dP_3–M_2 (P_2 and dP_4 alv.)	(I)	28248

F. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM COYOTE ROCK:

SKULL AND MANDIBLE		U.N.S.M.
Fragmentary skull with P^2–M^3 and partial mandible with P_3–M_3	(M+)	28556

FROM STEAMBOAT ROCK:

SKULL AND MANDIBULAR RAMUS		
Partial right side of skull with C/–P^1 rt. and P^2–M^3 and partial left ramus with P_2–M_3	(M+)	28557

G. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, MORRILL COUNTY, NEBRASKA

FROM LOWER PART OF GERING FORMATION, E. OF REDINGTON GAP (COLLECTED BY S. R. SWEET, 1936):

SKULL AND MANDIBLE		U.N.S.M.
Partial skull with C/–P^2 rt. and P^3–M^3 and partial mandible with P_1–P_3 rt. and P_4 (br.)–M_3	(W+)	28452

FROM WILDCAT RIDGE, U.N.S.M. COLL. LOC. MO–108:

MAXILLA AND MANDIBULAR RAMUS		
Partial right maxilla with P^4–M^3 and partial left ramus with M_2–M_3(br.)	(W+)	28231
Partial left maxilla with M^1–M^3	(W)	28553

FROM BRIDGEPORT AREA:

MANDIBULAR RAMUS, IMMATURE		
Partial left ramus with dP_2–M_1	(I)	28416

FROM 12 MI. S. OF BRIDGEPORT:

MANDIBULAR RAMUS		
Partial left ramus with P_1(br.)–M_3	(W)	28246

FROM 5 MI. N. AND 1 MI. W. OF BRIDGEPORT:

MANDIBULAR RAMUS		
Left ramus with I_1–P_1 alv. and dP_2–M_3(germ)	(I)	28415

4. **Leptauchenia parasimus,**[1] new species

From upper part of Gering Formation, Niobrara County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; Sioux, Sheridan, and Banner counties, Nebraska; and from Gering equivalent, Washabaugh County, South Dakota

DESCRIPTION

SKULL: Larger and more massive than in examples of *L. martini;* close to that of examples of *L. margeryae* in size and robustness; malar very deep below orbit; posterior palate extending for slight distance posterior to M^3.

MANDIBLE: Same size comparison as skull; more robust than in examples of *L. martini,* less robust than in *L. margeryae.*

DENTITION: Series longer, more robust, and more hypsodont than in *L. martini,* close to those of *L. margeryae* but less hypsodont.

LIMBS: Longer than in examples of *L. decora.*

MEASUREMENTS: Tables 12 and 15 (pp. 274 and 326).

ILLUSTRATIONS: Figures 33, 38, 40.

[1] *Para,* closely resembling, or similar to; and *simus,* the species *Cyclopidius simus.*

Discussion

It is unfortunate that the remains of *L. parasimus* are not in a better state of preservation. The holotype (inferior, anterior portion of skull) is more readily compared with examples of *L. margeryae* than with those of *L. martini*. The holotype lacks the nasal-facial vacuity and the occipital region. Referred F:A.M. 57151 has retained the orbits, the posterior border of the nasal-facial vacuity, and the complete occipital region. All these portions of the skull also seem closer to those of *L. margeryae* than to those of *L. martini*.

The F:A.M. specimens from Wyoming were collected by Nelson J. Vaughan, Gene Roll, Everett De Groot, John Lynch, and Charles H. Falkenbach, 1930–1955; the F:A.M. specimens from Nebraska and South Dakota, by Morris Skinner and associates, 1942 and 1949; and the U.N.S.M. collections, by C. Bertrand Schultz and associates, 1937, 1950.

Thirty specimens are here recorded:

HOLOTYPE

Inferior, anterior portion of skull with $C/–M^3$. (w$\ddagger^+$)	F:A.M. 34485	From upper part of Gering Formation, 8 mi. N. and 5 mi. E. of Lusk, Hat Creek Basin, Cheyenne River drainage, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933 Figures 33, 38

REFERRED FROM (A) NIOBRARA, (B) LARAMIE, AND (C) GOSHEN COUNTIES, WYOMING; (D) SIOUX, (E) SHERIDAN, AND (F) BANNER COUNTIES, NEBRASKA; AND (G) WASHABAUGH COUNTY, SOUTH DAKOTA

A. FROM NORTH PLATTE RIVER DRAINAGE, NIOBRARA COUNTY, WYOMING

From Little Muddy Creek:

3 skulls		F:A.M.
Partial skull with $C/–dP^1–M^3$ (germ, br.) ($P^3–P^4$ erupt.)	(I)	56801
Inferior, anterior portion of skull with $C/$(br.)$–M^3$	(w$\ddagger^+$)	56802
Skull with $P^1–dP^2–M^2$(germ)	(I)	56803

3 maxillae		
3 partial left maxillae with		
$M^1–M^3$(br.)	(w)	56804
dP^2(br.)$–M^2$	(I)	56805
$dP^1–M^2$(erupt., br.)	(I)	34489

4 mandibular rami		
Partial mandible with $I_2–I_3$ alv. and $/C–M_3$. Figures 33, 40	(M+)	45639
Partial right ramus with $P_2–P_3$ alv. and $P_4–M_3$ (M_1 br.)	(M)	56806
Left ramus with $I_2–dP_1–M_3$(germ) (P_2 br.)	(I)	56807
Partial left ramus with $M_1–M_2$	(w)	56808

From N. Ridge, N. of Jeriah:

5 mandibular rami		
Partial mandible with $I_1–M_3$ ($/C$ br., M_3 erupt.)	(M)	56809
Partial mandible with $P_4–M_3$	(w)	56810
Partial left ramus with M_3	(w+)	56811
Partial right ramus with $P_1–M_3$ (P_1 br., P_4 and M_3 erupt.)	(–M)	56864
Partial right ramus with M_2(br.)$–M_3$	(w+)	56865

B. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, LARAMIE COUNTY, WYOMING

From Tremain Area:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Partial skull with P^4–M^1 br. and M^2–M^3, mandible with /C(br.)–M_3, partial scapula, 2 partial femora, partial tibia, partial fibula, calcaneum, and partial pelvis . . .	(w)	57151

2 MAXILLAE

Partial right maxilla with dP^3–M^1	(i)	56813
Partial left maxilla with dP^3–M^1(erupt.)	(i)	56814

MANDIBULAR RAMUS

Partial left ramus with dP_3–M_2	(i)	57152

FROM E. OF U. S. HIGHWAY NO. 85:

MAXILLA

Partial left maxilla with P^3(br.)–M^2 (M^1–M^2 br.)	(w+)	56815

C. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, SOUTHWEST END OF 66 MOUNTAIN, GOSHEN COUNTY, WYOMING

MANDIBULAR RAMUS

		F:A.M.
Partial right ramus with M_1–M_3	(w+)	56816

D. FROM WHITE RIVER DRAINAGE U.N.S.M. COLL. LOC. SX–22, SIOUX COUNTY, NEBRASKA

SKULL AND MANDIBLE

		U.N.S.M.
Parts of skull with C/(br.)–dP^1–M^2 and partial mandible with P_1–dP_2–M_2	(i)	28558
Anterior left side of skull with C/–dP^2–M^2	(i)	28559

D′. FROM NORTH PLATTE RIVER DRAINAGE, JOE SANFORD RANCH, NORTH OF MITCHELL, SIOUX COUNTY, NEBRASKA

FROM JOE SANFORD RANCH, N. OF MITCHELL:

SKULL, IMMATURE

		F:A.M.
Posterior portion of skull with dP^3–M^2(erupt.)	(i)	56817

E. FROM WHITE RIVER DRAINAGE, 2½ MILES EAST OF WHITE CLAY, ALONG NEBRASKA-SOUTH DAKOTA STATE LINE, SHERIDAN COUNTY, NEBRASKA

SKULL

		F:A.M.
Partial skull with C/(br.)–M^3 (P^1–M^1 alv.)	(w‡+)	56818

F. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK BASIN, 1 MILE EAST OF WRIGHT GAP, BANNER COUNTY, NEBRASKA

SKULL AND MANDIBLE

		U.N.S.M.
Anterior, inferior portion of skull with P^1(rt.)–M^3 and mandible (attached) with P_2–M_3	(w‡)	28560

G. TENTATIVELY REFERRED FROM APPROXIMATE GERING FORMATION EQUIVALENT, WHITE RIVER DRAINAGE, 3½ MILES NORTHWEST OF WANBLEE,[1] WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE

		F:A.M.
Partial skull with dP^1–M^2 (dP^2 alv.) and mandible with P_1(br.)–dP_3–M_2 (P_2 absent)	(i)	57148

2 SKULLS

Skull with C/–M^3	(w)	57149
Skull with P^1–dP^3–M^2	(i)	57150

[1] From "165′ above 1st white layer."

5. **Leptauchenia margeryae**,[1] new species

From Monroe Creek Formation, Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming and Morrill County, Nebraska

DESCRIPTION

SKULL: Largest, widest, and latest (geologically) of the subgenus; depressed, more so than in other species of genus.

MANDIBLE: Most robust of genus; tendency toward a deeper symphysis than in other species of genus.

DENTITION: Series similar in over-all length to examples of *L. parasimus;* tendency to be slightly more hypsodont than in latter species.

LIMBS: (Known from immature fragmentary elements only).

MEASUREMENTS: Table 12 (p. 274).

ILLUSTRATIONS: Figures 33, 38, 40, 53.

DISCUSSION

Remains of *Leptauchenia parasimus* from the upper part of the Gering Formation have characters similar to those in examples of *L. margeryae* from the Monroe Creek Formation. There is a size difference in the skulls, however, with those of the latter species being somewhat larger and more depressed than those of *L. parasimus.*

The F:A.M. specimens from Wyoming were collected by Gene Roll, John Lynch, Everett De Groot, and Charles H. Falkenbach, 1930–1955; and the U.N.S.M. specimen from Nebraska was collected by E. L. Blue, C. Bertrand Schultz, and associates, 1937.

Fifty-three specimens are here recorded:

HOLOTYPE

Skull with C/–M^3 and mandible with /C–M_3. (W+)	F:A.M. 45632	From Monroe Creek Formation, below "white layer," Muddy Creek, North Platte River drainage, Niobrara County, Wyoming; collected by John J. Lynch, Everett De Groot, N. J. Vaughan, and Charles H. Falkenbach, 1935 Figures 33, 38, 40, 53

REFERRED FROM (A) NIOBRARA COUNTY, WYOMING, AND (B) MORRILL COUNTY, NEBRASKA

A. FROM NORTH PLATTE RIVER DRAINAGE, MUDDY CREEK, NIOBRARA COUNTY, WYOMING

		F:A.M.
2 ASSOCIATED INDIVIDUALS		
Inferior, anterior portion of skull with P^2–M^3 and partial right ramus with M_1–M_2	(W+)	56819A
Inferior, anterior portion of skull with P^2(rt.)–M^3 (P^3 rt., P^4–M^1 br.)	(M+)	56819B
6 ASSOCIATED INDIVIDUALS		
Inferior portion of skull with C/–M^3 and partial mandible with P_1–M_3	(W‡)	56821A
Left and right maxillae with P^1–M^3 and partial right ramus with M_1–M_3 br.	(W)	56821B
Partial left maxilla with P^2–P^4	(W+)	56821C
Partial left maxilla with M^1(br.)–M^2	(M)	56821D
Partial right ramus with P_2–M_3	(W+)	56821E
Partial left ramus with M_1–M_3	(W+)	56821F
Symphysis with I_1–dP_4	(I)	56821G
2 ASSOCIATED INDIVIDUALS		
Partial right maxilla with P^2–M^3 and mandible with I_1–P_2 rt. and P_3(br.)–M_3	(W‡+)	56822A
Partial mandible with P_3–M_3	(W‡+)	56822B

[1] Named in honor of Mrs. Margeryie Falkenbach, wife of the late Charles H. Falkenbach, who over the years has given considerable assistance and encouragement to her husband with aid in the field as well as in the home.

4 ASSOCIATED INDIVIDUALS		F:A.M.
Anterior portion of skull with P^2–M^3(erupt.) (P^2–P^4 erupt., M^1 alv.)	(I)	56823A
Inferior, anterior portion of skull with I^2–M^3	(W+)	56823B
Partial mandible with I_3(rt.)–M_2 (P_1 alv., P_2–P_4 erupt.)	(I)	56823C
It is possible that the above A and C specimens are of one individual.		
Anterior portion of skull with C/–P^1 rt. and P^2–M^3(erupt.) and mandible with I_1–M_3 (erupt.) (P_2–P_4 erupt.)	(I)	56823D

2 ASSOCIATED INDIVIDUALS

Skull with C/–dP^1–M^2 and mandible with I_2–dP_2–M_2 (I_3 alv.)	(I)	56824A
Skull with C/–M^3 and mandible with I_3–P_1 rt. and P_2(alv.)–M_3	(M+)	56824B

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with dP^2, mandible with P_1–P_2 alv. and P_2–dP_4–M_2, partial humerus, partial radius, partial ulna, partial manus, and vertebrae	(I)	56825

4 SKULLS AND MANDIBLES

Fragmentary skull with M^3 br. and partial mandible with I_3–P_1 rt. and P_2–M_3 (P_4–M_2 br.)	(M+)	56826
Partial skull with C/–dP^3–M^2(germ) (P^1–P^2 rt.) and mandible with I_3–P_1 rt. and P_2 (alv.)–M_3	(I)	56827
Inferior, anterior portion of skull with P^4–M^1 alv. and M^2–M^3 and right ramus with P_1–M_3	(W‡)	56828
Partial skull with dP^3–M^2(erupt.) and partial mandible with I_3–dP_2–M_1(br.)	(I)	56829

8 SKULLS

8 partial skulls with		
C/–dP^2–M^2(erupt.)	(I)	56830
I^3–M^3. Figure 33	(W+)	56831
C/–M^3	(W+)	56832
P^2–P^3 rt. and P^4–M^3	(W+)	56833
C/–P^1 rt. and P^2–M^2	(W+)	56834
C/(rt.)–M^3	(M+)	56835
C/–M^3	(W)	56836
P^2–M^3	(W+)	56837

MAXILLA AND MANDIBULAR RAMUS

Partial left maxilla with P^3(rt.)–M^3 and partial left ramus with M_1(rt.)–M_3	(W+)	56838

6 MAXILLAE

6 partial right maxillae with		
P^4–M^3	(M+)	56839
P^4–M^3	(M+)	56840
M^1–M^3	(W+)	56841
M^1–M^3	(W+)	56842
dP^3–M^1	(I)	56843
C/(germ)–dP^3–M^1 (P^1–P^2 rt.)	(I)	57122

9 MANDIBLES

9 partial mandibles with		
I_1(rt.)–dP_2–M_2	(I)	56844
/C–M_3	(M+)	56845
I_1–I_3 alv. and /C(rt.)–M_3	(W)	56846
I_3(br.)–M_3	(W+)	56847
I_1–I_3 rt. and dP_2–M_2	(I)	56848
P_3–M_3	(M)	56849
P_1(br.)–M_2 (P_3–P_4 erupt.)	(–M)	56850
I_3–/C br and P_1–dP_2–M_2	(I)	56851
P_1(br.)–M_3 (P_2–P_4 erupt.)	(–M)	56852

5 MANDIBULAR RAMI		F:A.M.
3 partial right rami with		
/C–P_2 rt. and P_3–M_3	(w+)	56853
I_1–M_3	(w)	56854
/C–P_1 rt. and P_2–M_3	(w‡)	56855
2 partial left rami with		
P_4–M_3	(w+)	56856
P_2–M_3	(w)	56857

B. FROM NORTH PLATTE RIVER DRAINAGE, 4–5 MILES NORTHEAST OF BRIDGEPORT, MORRILL COUNTY, NEBRASKA

MANDIBLE		U.N.S.M.
Partial mandible with /C(rt.)–M_3 (P_1–P_3 alv.)	(w+)	28264

V. CYCLOPIDIUS Cope

Cyclopidius Cope, 1878a, p. 221.

Brachymeryx Cope, 1878a, p. 220; 1884, pp. 504, 546.

Genotype: *Cyclopidius simus* Cope.

Skull: Small in size (slightly larger than in examples of largest of species of *Leptauchenia*), basal lengths ranging from 111 to 125 mm.; widths from 93 to 96 mm.; brachycephalic; sagittal crest prominent; brain case depressed; nasal-facial vacuity comparatively short (anteroposteriorly) and wide (laterally), posterior border opposite mid-portion of orbit; bulla inflated, more so than in *Leptauchenia.*

Mandible: Light, tendency to be lighter than in examples of Miocene species of *Leptauchenia* and *Hadroleptauchenia.*

Dentition: Subhypsodont; dental formula I^2_3–M^3_3; light, lighter than that of *Leptauchenia margeryae* (largest species of *Leptauchenia*) or any examples of Miocene species of *Hadroleptauchenia.*

Limbs: (Unknown).

Measurements: Table 12 (p. 274).

Illustrations: Figures 34, 38, 40, 41.

Discussion

In the original description of *Cyclopidius,* Cope[1] gave the formula for the incisors as I^2_2, and Thorpe[2] recorded it as I^2_{2-3}. There is no evidence, however, of only two lower incisors in any of the available examples of *Cyclopidius.* In fact, the evidence at hand demonstrates that all species of the Leptaucheniinae have three lower incisors. There appear to be, however, only two upper incisors present in the Miocene species of the various genera of the tribe Leptaucheniini, whereas there are three upper incisors present in the various species of the tribe Sespiini (known only from the lower Miocene). It is questionable whether there are any species of Oligocene leptauchenins which have only two upper incisors. All Oligocene examples available to the present writers have three incisors. Unfortunately, incisors are not preserved in the majority of the skulls and mandibular rami.

Cope[3] reported concerning *Cyclopidius:* "This genus is related to *Leptauchenia* Leidy, but differs in having but two lower incisors below. That genus [*Leptauchenia*] belongs to a lower horizon, the Miocene [= Oligocene-Miocene] of White River, while the present form [*Cyclopidius*] is its successor in the upper Miocene [= lower Miocene] or Loup Fork beds." The present writers agree with Cope that *Cyclopidius* is related to *Leptauchenia* but consider that the genus *Leptauchenia* represents a continuous line of development in the central Great Plains from late Brule times ("Zone C" of Brule) through Monroe Creek times. The genus *Cyclopidius,* however, does not appear to be represented in the central Great Plains region but is recorded only from the northern Great Plains (Montana) and is known from deposits approximately equal to the Gering of Nebraska.

Schlaikjer's[4] phylogenetic chart for the species of *Leptauchenia* and *Cyclopidius* differs radically from that of the present writers (see chart 8, p. 228). He restricted the genus *Leptauchenia* to the Oligocene, except for "*L.*

[1] 1878a, p. 221.

[2] 1937, p. 25, fig. 2.

[3] Thorpe, 1937, p. 256.

[4] 1940, p. 692.

minora" (= *Sespia nitida*) which he recorded from the "L. Harrison." The present writers have not seen evidence of leptauchenins in the Harrison Formation or its equivalent in other localities (including the Middle and Upper John Day deposits). Schlaikjer's "L. Harrison," in connection with the leptauchenin remains in the Goshen Hole area, is equal to the upper part of the Gering Formation of western Nebraska. It is interesting to note that the type locality of the Gering Formation[1] is less than 20 miles east of Goshen Hole, and the deposits can be correlated physically. Also the oreodont faunas of the upper Gering of Nebraska are similar to those of equivalent deposits in Goshen Hole in eastern Wyoming.

Schlaikjer included various species under the genera *Leptauchenia* and *Cyclopidius* which are generically distinct from either. An evaluation by the present writers of his conclusions concerning the taxonomy and geologic ages of these species is as follows:

"*L. decora* from U. Brule" (=*L. decora* from "Zone D" of Brule)
"*L. nitida* from U. Brule" (=*Sespia nitida* from upper Gering)
"*L. major* from U. Brule" (=*Pseudocyclopidius major* from lower Gering)
"*L. minora* from L. Harrison" (=*L. nitida* from upper Gering)
"*C. brevifacies* from L. Harrison" (=*Pithecistes brevifacies* from Gering equivalent)
"*C. schucherti* from L. Harrison" (=*L. decora* from "Zone D" of Brule)
"*C. simus* from L. Harrison" (=*C. simus* from Gering equivalent)
"*C. densa* from L. Harrison" (=*Hadroleptauchenia densa* from upper Gering)
"*C. lullianus* from L. Harrison" (=*Pseudocyclopidius lullianus* from upper Gering)
"*C. californica* from L. Harrison" (=*Sespia californica* from Gering equivalent)
"*C. heterodon* from L. Harrison" (=*Sespia heterodon* from Gering equivalent)

Thorpe[2] published a phylogenetic chart of the oreodonts, which included the genera *Leptauchenia* and *Cyclopidius*. This also is quite distinct from both Schlaikjer's chart and chart 8 in the present paper (p. 228). Thorpe considered that there was a single line of development from late Oligocene to middle Miocene, rather than several parallel phyla developing independently. He also thought that his "*Cyclopidius* (*Chelonocephalus*) *schucherti*" was from the "Middle Miocene (Sheep Creek),"[3] and represented the end of the *Leptauchenia-Cyclopidius* line, but in reality this species is synonymous with *Leptauchenia decora* from the upper Oligocene (faunal "Zone D" of the Brule). (See p. 278 for further discussion of the validity of "*C.* (*C.*) *schucherti*" of Thorpe.)

Scott,[4] in a discussion of *Leptauchenia*, considered that *Cyclopidius* was a Miocene genus. He also concluded that *Leptauchenia-Cyclopidius-Pithecistes* was one "genetic series." The present writers, of course, believe that the three genera represent distinct phyla which paralleled one another in development during late Oligocene and early Miocene times (see chart 8, p. 228). All three genera are very closely related and must have been derived from a common ancestor early in Oligocene times, although *Cyclopidius* may have branched off from the *Leptauchenia* phylum later in the Oligocene, or perhaps as late as early Miocene. Some taxonomists may wish to consider both *Pithecistes* and *Cyclopidius* as subgenera of *Leptauchenia*, but the present writers wish to retain these already established genera, as the characters seem to warrant the division.

As far as is known, examples of both *C. simus* and *C. emydinus* come from deposits equal in age to the upper part of the Gering. Such occurrence is supported by other oreodonts (previously reported in this revision) from Montana. The leptauchenins are not known to have occurred in deposits above the Monroe Creek or its equivalent in age. No deposits or faunas have been recorded from Montana that are referable to the Monroe Creek. This evidence (or lack of it) indicates Gering age for both these species.

It is possible, but hardly probable, that lower Gering deposits are present in Montana. Perhaps the thickness of the Gering age deposits may account for *C. simus*, the smaller form, which could have come from a lower part of a Gering equivalent. *Cyclopidius emydinus*, the larger form, may have come from the upper portion.

A second possible conclusion is that *C. simus*

[1] Darton, 1903a, p. 33, fig. 11.
[2] 1937, p. 25, fig. 2.
[3] Thorpe, 1937, p. 256.
[4] 1940, p. 692.

and *C. emydinus* represent two separate phyla, both forms occurring at the same time.

Cyclopidius simus is close in size to examples of *Leptauchenia parasimus,* and *C. emydinus* is close to *Hadroleptauchenia densa,* but both Montana forms have decidedly lighter dentitions. There are no leptauchenins from the Great Plains that compare with *Cyclopidius* examples from Montana. The present writers believe that *C. simus* and *C. emydinus* represent two separate phyla that developed independently from those of the Great Plains. There is, however, one species from Montana, *quadratus,* that the present writers have referred to *Pseudocyclopidius,* a new genus well represented in the central Great Plains.

Distribution

Two species of *Cyclopidius* are here recorded from the lower Miocene (Gering Formation equivalent in part) of Montana. (See geologic distribution, chart 8, p. 228.)

Summary of Species and Types

Two species of *Cyclopidius* from two lower Miocene localities are here recorded:

1. *C. simus* Cope, from Montana; referred remains from Meagher and Lewis and Clark counties, Montana. (Approximately equal in age to the upper Gering.)

Holotype: Partial skull, A.M. 8116. Figures 34, 38.

2. *C. emydinus* Cope, from Montana; referred remains from Meagher, and Lewis and Clark counties, Montana. (Approximately equal in age to the upper Gering.)

Holotype: Skull, A.M. 8115. Figures 34, 38, 41.

DETAILED LIST OF TYPE, REFERRED SPECIMENS, AND SYNONYMY

CYCLOPIDIUS

Total available specimens: 55

1. Cyclopidius simus Cope

From deposits approximately equal in age to the upper part of the Gering Formation, "Deep River," Montana; referred remains from Meagher and Lewis and Clark counties, Montana

Cyclopidius simus Cope, 1878a, p. 221. Matthew (in part), 1899b, p. 73. Schlaikjer, 1935, p. 166, pl. 76, fig. 26. Thorpe, 1937, p. 249, pl. 37, figs. 10–11, pl. 38, figs. 1–2.

Brachymeryx feliceps Cope, 1878a, p. 220; 1884b (*B. feliceps* = *C. simus*), p. 558. Thorpe, 1937 (*B. feliceps* = *C. simus*), p. 254, pl. 38, figs. 9–10.

Pithecus decedens Cope, 1884a, p. 558.

Cyclopidius decedens (Cope): Matthew, 1899b, p. 73. Thorpe (= ?*C. simus*), 1937, p. 252, pl. 38, fig. 4.

Cyclopidius (*Pithecistes*) *decedens* (Cope): Loomis, 1925a, p. 248.

Cyclopidius incisivus Scott, 1893, p. 661; 1895, p. 163. Loomis, 1925a, p. 248 (= *C. "emydinus"* according to Loomis). Thorpe (= ?*C. simus*), 1937, p. 255, pl. 38, figs. 6–8.

Characters

Skull: Within size range of that of *Leptauchenia margeryae;* smaller than that of holotype of *C. emydinus;* differs from that of *C. emydinus* as follows: greater posterior invasion by nasal-facial vacuity, auditory bulla less inflated, and shorter distance from posterior border of M^3 to posterior border of condyle (= 59 mm.; in *C. simus,* 76.5 mm.)

Mandible: Same relative measurements as skull; lighter with less depth to ramus than in *C. emydinus.*

Dentition: Similar to that of *C. simus.*

Limbs: (Unknown).

Measurements: Table 12 (p. 274).

Illustrations: Figures 34, 38, 40.

Discussion

Matthew[1] reviewed the several leptauchenins described by Cope and stated, "*Pithecistes decedens* is the permanent and *P.* [= *Sespia*] *heterodon* probably the milk dentition of a smaller species [than *simus*] of *Cyclopidius.*" Actually Matthew's conclusions are reversed in that *P. decedens* has dP^3–M^1 (immature), and *S. heterodon contains* P^4–M^1 (mature). Loomis[2] concluded, "I therefore consider not only *Brachymeryx feliceps* and *Pithecistes breviceps,* but also *C.* (*Pithecistes*) *decedens* and *C.* (*Pithecistes*) *heterodon* as synonyms of *C. simus.*" Actually three distinct species representing different phyla are involved.

[1] 1899a, p. 73, footnote 2.
[2] 1925a, p. 248.

Schlaikjer[1] also concluded that Matthew was in error and agreed with the present writers in regard to the dentitions of the species *decedens* and *heterodon.* Thorpe[2] came to the same conclusions that the teeth of "*C. decedens*" were dp^3–M^1 and not P^4–M^2 as considered by Cope. He also placed the form in synonymy with *C. simus.* (See discussion under *Pithecistes,* p. 259.)

Loomis[3] under a discussion of *Cyclopidius* Cope, stated, "In the Deep River material I can find but two types of *Cyclopidius,* one with a short snout . . .; the other with a longer snout, . . . *C. emydinus* illustrates the long snouted type, and I can see nothing to distinguish *C. incisivus* from it, so I consider the latter as a synonym of the former." This statement implies that *C. simus* represents a short-snouted type, which appears to be the case.

Thorpe[4] discussed Loomis' conclusions and reported: "Loomis grouped all of the Deep River forms into two types, the short-faced, headed by *C. simus,* and the long-faced, with *C. emydinus* as the example. In the known skull types from which we can get dimensions, the indices of length of face in front of the orbits to the total skull length work out as follows: *C. emydinus,* 0.258, and *C. simus,* 0.322 (. . . probably more complete skulls would show a closer agreement in indices)." The present writers agree with Thorpe in thinking that the two type specimens do not represent a sufficient number of examples as a basis for indices.

Schlaikjer,[5] on an examination of the holotype of *Cyclopidius simus* and *C. emydinus,* concluded that he was "unable to observe any character or characters in *C. emydinus* which distinguish it specifically from *C. simus.*" Thorpe[6] concluded that *simus* and emydinus were possible synonyms and stated: "In my opinion, arrived at several years ago, the differences between this species [*emydinus*] and *C. simus* are not in the main too great to be explained on the basis of age and sex. Recently Schlaikjer (1935, p. 166) enumerated Cope's distinctions between the two and showed that he also came to the same conclusions as I did. However, there is a difference between us in the position of the palatonarial border, which in *C. simus* lies several millimeters behind the line of the posterior edges of the lost molars."

The workers quoted above seem, however, to have ignored the fact that the two holotypes (skulls) show a definite difference in the distance between the posterior border of M^3 to the anterior border of the auditory bulla. In *C. simus* this measurement is 59 mm.; in *C. emydinus* it is 76.5 mm. This character appears to be a reliable one throughout the leptauchenins. The skull of *C. simus* appears to be short, as do other examples of the subgenus, but that of *C. emydinus* is comparatively long. The dentitions of the two species, however, are similar. Until more evidence is available, the present authors prefer to consider *C. emydinus* a species distinct from *C. simus.* (See discussion, p. 302).

Forty-eight specimens are here recorded:

HOLOTYPE

Partial skull with P^2–M^3. (w+)	A.M. 8116	From deposits approximately equal in age to upper part of Gering Formation, "Deep River" beds, "Smith Creek,"[7] Montana; collected by J. C. Isaac, 1877 Figured by Schlaikjer, 1935, pl. 7, fig. 3; Thorpe, 1937, pl. 38, fig. 4 This report, figures 34, 38

[1] 1935, p. 165.
[2] 1937, p. 252.
[3] 1925a, p. 247.
[4] 1937, p. 254.
[5] 1934, p. 166.
[6] 1937, pp. 252–253.
[7] The specimen apparently came from the lower part of the "Deep River" Formation, Smith River Valley (= "Smith Creek" of Cope), Meagher County, but the exact locality and geologic horizon are unknown.

REFERRED FROM (A) TYPE AREA, MONTANA; (B) MEAGHER AND (C) LEWIS AND CLARK COUNTIES, MONTANA

A. FROM SAME GENERAL AREA AS HOLOTYPE, ?MEAGHER COUNTY, MONTANA (COPE COLLECTION)

SKULL		A.M.
Inferior, anterior portion of skull with C/–dP^2–M^2	(I)	8126

The above specimen is the holotype of "*Brachymeryx feliceps*" Cope. Figured by Thorpe, 1937, pl. 38, figs. 9–10.

2 MAXILLAE		
Left maxilla with C/–M^3	(w)	8125
Partial right maxilla with dP^3(rt.)–M^1	(I)	8130

The above specimen is the holotype of "*Pithecistes decedens*" Cope. Figured by Thorpe, 1937, pl. 33, fig. 4.

3 MANDIBULAR RAMI		
Left ramus with I$_3$–M$_3$. Figure 40	(w)	8117
Figured by Thorpe, 1937, pl. 37, figs. 10–11.		
Partial right ramus with M$_1$–M$_3$	(w+)	8121
Partial right ramus with I$_1$–dP$_2$–M$_2$ (I$_1$–dP$_4$ rt.)	(I)	8122

B. FROM SMITH RIVER VALLEY, MEAGHER COUNTY, MONTANA

FROM WHITE SULPHUR SPRINGS AREA (COLLECTED BY H. E. KOERNER, 1935 AND 1937):

5 SKULLS		Y.P.M.
Anterior portion of skull with C/–M^3	(w+)	10415
The above specimen was collected by Charles H. Falkenbach and presented to the Yale Peabody Museum by the Frick Laboratory.		
Inferior, anterior portion of skull with C/–P^1–dP^2–M^2	(I)	13980
Inferior, anterior portion of skull with I^2(alv.)–dP^2–M^2(erupt.)	(I)	13981
Inferior, anterior portion of skull with C/–M^3	(w‡)	13992
Inferior, anterior portion of skull with C/–M^3	(w)	13994

6 MAXILLAE		
3 right maxillae with		
P^1–dP^2–M^1	(I)	13975
C/–M^2.	(w)	13983
P^1–dP^2–M^2	(I)	13984
3 left maxillae with		
C/–M^1(br.)	(w)	13982
C/–M^2	(w+)	13991
C/–M^3.	(w‡)	13993

10 MANDIBULAR RAMI		
4 mandibles with		
I$_1$(alv.)/dC–M$_1$ (I$_3$ erupt.)	(I)	13979
I$_2$–M$_3$ (M$_1$ br.)	(w+)	13985
I$_2$–M$_2$	(w‡)	13984
/C–M$_3$	(w‡)	13998
4 right rami with		
dP$_4$(br.)–M$_1$	(I)	13971
dP$_4$–M$_2$	(I)	13972
P$_1$–M$_3$	(w+)	13987
P$_3$(alv.)–M$_3$(erupt.)	(M+)	13997
2 left rami with		
P$_1$–P$_3$ alv. and dP$_4$(br.)–M$_2$(br.)	(I)	13976
P$_4$–M$_3$	(w‡)	13988

FROM WHITE SULPHUR SPRINGS AREA, "LOW" (COLLECTED BY CHARLES H. FALKENBACH, 1936):

2 MANDIBULAR RAMI

		F:A.M.
Partial symphysis with I_1–/C rt. and P_1	(w)	57163
Partial right ramus with M_3	(w)	57164

FROM LONE BUTTE, 2 MI. SE. OF WHITE SULPHUR SPRINGS (COLLECTED BY J. LEROY KAY, 1943):

SKULL AND MANDIBLE

		C.M.
Inferior, anterior portion of skull with C/–M^3 and partial mandible with I_1–M_3	(w)	9200

The above specimens listed under three numbers belong to the same individual.

3 PARTIAL SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Partial left maxilla with dP^1–dP^4, mandible with I_2–I_3 alv. and /C–dP_2–M_1	(I)	9280
Partial right ramus with dP_4–M_2(erupt.)	(I)	9280
2 partial ulnae		9280

At least two individuals are represented in the above material listed under the same number.

Inferior, anterior portion of skull with P^1–dP^2–M^1(erupt.), partial mandible with dP^4–M^1, partial radius, and partial ulna	(I)	9339

SKULL

Inferior, anterior portion of skull with P^1–dP^2–M^1(br.)	(I)	9283

3 MANDIBULAR RAMI

Partial right ramus with dP_4(br.)–M_2	(I)	9284
2 partial left rami with		
dP_3–M_3(germ)	(I)	9282
I_3–P_1(br.)–dP_2–M_3(erupt.)	(I)	9285

FROM "SMITH RIVER VALLEY" (COLLECTED BY R. A. STEVENSON, 1891):

SKULL

		P.U.
Inferior, anterior portion of skull with I^2–M^3	(W+)	10473

The above specimen is the holotype of "*Cyclopidius incisivus*" Scott. Figured by Thorpe, 1937, pl. 38, figs. 6–8.

C. FROM MISSOURI RIVER VALLEY, CANYON FERRY, LEWIS AND CLARK COUNTY, MONTANA (COLLECTED BY EARL DOUGLASS, 1902)[1]

MAXILLAE AND MANDIBULAR RAMI

		C.M.
Partial left and right maxillae with P^4–M^3 and partial right ramus with I_1–P_2 alv. and P_3–M_3	(W+)	1298

4 SKULLS

4 inferior, anterior portions of skulls with		
C/–M^3	(M)	1296
I^2–M^3	(W+)	1313
I^1(alv.)–M^3	(M)	1314
C/–M^3	(M+)	1322

5 MANDIBULAR RAMI

Partial mandible with P_2–dP_3–M_2	(I)	1297
Partial mandible with P_4–M_3 (M_1–M_2 br.)	(W‡+)	1299
Partial right ramus with P_4–M_3	(W+)	1297

[1] White, 1954, p. 426, recorded the following three specimens from Canyon Ferry, U.S.N.M. Coll. Loc. 24 LC 18: skull and jaws (U.S.N.M. 19806), skull and jaws (U.S.N.M. 19088), and right mandible with dP_2–M_2. The present writers have not seen the specimens, but White identified them as *Cyclopidius simus*.

		F:A.M.
Partial symphysis with P_1 and P_2–P_3 rt.	(w+)	57163
Partial right ramus with M_3	(w+)	57164

The above two F:A.M. specimens were collected by Charles H. Falkenbach.

2. **Cyclopidius emydinus** Cope

From deposits approximately equal in age to upper part of Gering Formation, "Deep River" beds, Smith River Valley, Montana; referred remains from Meagher and Lewis and Clark counties, Montana

Cyclopidius emydinus COPE, 1884a, p. 553; 1888, pl. 28. SCOTT 1890b, pl. 15, figs. 71–19. ZITTEL, 1893, p. 356, fig. 29.

Cyclopidius simus COPE: SCHLAIKJER (in part), 1935, p. 165, pl. 26, fig. 1.[1]

Cyclopidius emydinus Cope (= ?*C. simus*): THORPE, 1937, p. 252, figs. 180–182.

CHARACTERS

SKULL: Longer distance from posterior border of M^3 to anterior border of auditory bulla than in *C. simus.* (Distance in *C. simus,* 59 mm.; in this species, 76.5 mm.)

MANDIBLE: Tendency for rami to be deeper below anterior border of M_3 than those in *C. simus.*

DENTITION: Similar to that of *C. simus.*

LIMBS: (Unknown).

MEASUREMENTS: Table 12 (p. 274).

ILLUSTRATIONS: Figures 34, 38, 40, 41.

DISCUSSION

The skull of *C. emydinus* has a longer distance between the posterior border of M^3 and the anterior border of the auditory bulla, and in this respect differs considerably from the skull of *C. simus* which is considered to have a comparatively short skull similar to examples of *Leptauchenia.*

The leptauchenins from Montana may well represent forms that evolved independently from those of the central Great Plains. *Cyclopidius simus* and *C. emydinus* dentitions tend to be lighter than those of the central Great Plains examples. (See discussion, under genus, p. 298.)

Local independent phyla of a genus are present also in the genus *Brachycrus.*[2] In Nebraska the sequence is from large to small-sized skulls, whereas in Wyoming the reverse is evident, with the sequence from small to large. The *Brachycrus* skulls from California are more robust than others of the genus. However, it would be impossible to separate these forms (from the three widely separated areas) into several genera; they are all *Brachycrus.*

Under *C. simus* (p. 298), the relationship of the various Montana leptauchenins is discussed. Schlaikjer considered *simus* and *C. emydinus* as synonyms. Thorpe questioned the synonymy. (See discussion, p. 299.)

It should be noted that the Montana leptauchenin species are distinct from the central Great Plains forms. In fact there is no evidence at hand that any of the Montana oreodonts are specifically the same as those of the central Great Plains.

Five specimens are here recorded:

HOLOTYPE

Skull with C/(br.)–M^3 (w‡)	A.M. 8115	From deposits approximately equal in age to upper part of Gering Formation, "Deep River" beds, "Smith Creek,"[3] Montana; collected by J. C. Isaac, 1877 Figured by Scott, 1890, pl. 15, figs. 17–19; Zittel, 1893, fig. 291; Schlaikjer, 1935, pl. 26, fig. 1; Thorpe, 1937, figs. 180–182 This report, figures 34, 38, 41

[1] Schlaikjer (1935, p. 167) stated, "... *C. emydinus,* ... is equivalent to *C. simus,*" but the caption of his plate 26, figure 1, reads "*Cyclopidius emydinus.*"

[2] Schultz and Falkenbach, 1940, p. 227.

[3] The specimen apparently came from the lower part of the "Deep River" Formation, Smith River Valley (= "Smith Creek" of Cope), Meagher County.

REFERRED FROM SMITH RIVER VALLEY, EXPOSURES WEST OF WHITE SULPHUR SPRINGS, MEAGHER COUNTY, MONTANA

4 MANDIBULAR RAMI		F:A.M.
Partial right ramus with I_2–M_3 (P_1–P_4 br.) Figure 34	(w+)	56960
		Y.P.M.
Partial right ramus with dP_3–M_2(erupt.)	(I)	13974
Partial right ramus with dP_4–M_1–M_2	(I)	13977
Partial right ramus with P_2–M_2 (P_4 br.)	(w)	13978

VI. HADROLEPTAUCHENIA, NEW GENUS

GENOTYPE: *Hadroleptauchenia shanafeltae*, new species.

DESCRIPTION

SKULL: Small in size[1]; basal lengths from 101 to 120 mm., widths from 82 to 114 mm.; mesocephalic to brachycephalic; moderately low; sagittal crest moderately prominent, less so than in examples of *Pseudocyclopidius;* frontals moderately wide, tending to be narrower than in examples of *Pseudocyclopidius;* nasals with only slight anterior retraction; orbit small, smaller than in examples of *Pseudocyclopidius*, looking outward, forward, and upward; malar moderately deep below orbit; zygomatic arch with a wide U-shaped superior border; infraorbital foramen above P^3; lacrimal fossa shallow, more so than in examples of *Pseudocyclopidius;* nasal-facial vacuity extending posterior to a point above posterior portion of M^2 to anterior portion of M^3; prominent depression or pit on face above premolars; auditory bulla well inflated, subround in shape, smaller than in examples of *Pseudocyclopidius*.

MANDIBLE: Moderately light; postsymphysis below P_4; mandibular ramus moderately shallow; inferior border of ramus with slight downward slope posteriorly to a point below M_3, with a noticeable concave notch beyond this point; ascending ramus of medium height.

DENTITION: Subhypsodont, less hypsodont than examples of *Pseudocyclopidius;* dental formula $\frac{3-2}{3}, \frac{1}{1}, \frac{4}{4}, \frac{3}{3}$; premolars not crowded; external styles of superior molars moderately prominent, less massive than in examples of *Pseudocyclopidius*, tendency for length of premolar series over molar series to be less than in examples of *Pseudocyclopidius*.

LIMBS: Short and light compared with those of *Pseudocyclopidius*.

MEASUREMENTS: Tables 13 and 15 (pp. 304 and 326).

ILLUSTRATIONS: Figures 34, 35, 38, 40, 53, 55 (skulls, mandibular rami), and 43 (limbs).

[1] Examples of *Hadroleptauchenia* are noticeably smaller than those of *Pseudocyclopidius* from the same geologic deposits.

DISCUSSION

The skulls of *Hadroleptauchenia* are intermediate in size between those of *Leptauchenia* (smaller) and those of *Pseudocyclopidius* (larger) which come from geological deposits of the same age. For example, *H. shanafeltae* from the lower Gering is definitely larger than *L. martini* and smaller than *P. major* also from the lower Gering. In "Zone D" of the Brule, however, there is less differentiation in size between the species representing the three phylogenetic lines. The skulls of *Hadroleptauchenia* are distinct from those of *Pseudocyclopidius* in possessing the following characters: shorter muzzle; frontals narrower above orbits; and proportionately shorter premolar series (anteroposteriorly). The limb elements of this genus are noticeably shorter and lighter than examples of *Pseudocyclopidius* but larger than those of *Leptauchenia*.

The three phyla mentioned above are closely related lines which paralleled one another in the development of various characters. It is very evident, however, that the development did not take place at the same rate in each phylum. The rate of evolutionary change in the *Pseudocyclopidius* line was more rapid than in *Hadroleptauchenia*, but the rate of change in the latter line took place more rapidly than in *Leptauchenia*. It might also be said that this trend started at an earlier geological time in *Pseudocyclopidius* than in the other two genera. Of the three phyla, it is obvious that *Leptau-*

TABLE 13

Hadroleptauchenia, New Genus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*H. eiseleyi*, new species[b]	*H. primitiva*, new species	*H. shanafeltae*, new species	*H. densa* Loomis		*H. extrema*, new species
	Holotype U.N.S.M. 28208	Holotype F:A.M. 45577	Holotype U.N.S.M. 1082	Holotype A.C. 7695	Referred F:A.M. 37525	Holotype F:A.M. 45602
Stage of wear of teeth	(w)	(w+)	(w‡)	(M+)	(w)	(w‡)
Length (incl. supraoccipital crest and incisors)	—	((117))	123	(132)	(130)	(140)
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	—	(106)	107	(115)	(115)	—
Width (max.)	—	87	89	—	94.5	(100)
Width of brain case (max.)	—	((42))	40	39	39	44
Width, interorbital (min.)	—	(40)	41.5	(45)	48	53
Distance from anterior rim of orbit to anterior base of C/	—	40	40.5	44.5	45	48
Distance from anterior rim of orbit to supra-occipital crest	—	(82)	84	93	91	98
Width of muzzle at infraorbital foramina	—	37	38	(37.5)	39	44
Width across canines	—	22	25	(22)	22.5	(25)
Length, C/–M^3 incl.	—	(61)	64	69.5	69	(68)
Length, P^1–M^3 incl.	—	54.5	57.5	61.5	62.5	62
Length, P^1–P^4 incl.	—	24	24.5	24.5	25	25
Length, M^1–M^3 incl.	28.5	33	34.5	41	40.5	38.5
Width of M^3 (max.)	(11)	14	16	14.5	14	14.5
Depth of malar below orbit	—	18	22.5	22.5	20	24

TABLE 13—(*Continued*)

MANDIBULAR RAMUS	*H. eiseleyi*, new species	*H. primitiva*, new species	*H. shanafeltae*, new species	*H. densa* Loomis		*H. extrema*, new species
	Holotype U.N.S.M. 28208	Holotype F:A.M. 45577	Holotype U.N.S.M. 1082	Holotype A.C. 7695	Referred F:A.M. 37525	Referred F:A.M. 56973
Stage of wear of teeth					—	(w)
Length (max., incl. incisors)	—	—	(109)	—	—	(119)
Length, /C-condyle incl.	—	—	(94)	—	—	—
Depth of jaw under coronoid	—	—	66	—	60	—
Depth of jaw below anterior edge of M_3	—	—	28	—	28	29
Length, /C–M_3 incl.	—	—	—	—	—	71.5
Length, P_1–M_3 incl.	—	—	59.5	—	—	67.5
Length, P_1–P_4 incl.	—	—	20.5	—[c]	—	23
Length, M_1–M_3 incl.	—	—	39.5	—	44	43.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] Geologic variety example F:A.M. 45646 is an immature maxilla.
[c] Length of P_1–dP_4 incl., 31 mm.

chenia remained the most conservative in development.

DISTRIBUTION

Remains of *Hadroleptauchenia* have the greatest geologic distribution of all the leptauchenins. Five species and a geologic variety come from the middle and upper Oligocene (Brule) and lower Miocene (Gering and Monroe Creek formations) of Nebraska, Montana, South Dakota, and Wyoming. (See geologic distribution chart, p. 22.)

SUMMARY OF SPECIES AND TYPES

Five species and a geologic variety of *Hadroleptauchenia* from 19 upper Oligocene and 33 lower Miocene localities are here recorded:

1. *H. eiseleyi,* new species, from Scotts Bluff County, Nebraska. (Oreodont faunal "Zone A" of Brule Formation.)

HOLOTYPE: Partial maxilla, U.N.S.M. 28208. Figures 35, 38.

1a. *H. eiseleyi,* geologic variety, from Shannon County, South Dakota. ("Zone B" of Brule.)

EXAMPLE: Partial maxilla, F:A.M. 45646.

2. *H. primitiva,* new species, from Washabaugh County, South Dakota; referred remains from Washabaugh, Jackson, Shannon, and Fall River counties, South Dakota; and Sioux, Scotts Bluff, and Morrill counties, Nebraska. ("Zone D" of Brule.)

HOLOTYPE: Skull and mandible, F:A.M. 45577. Figures 35, 38, 53.

3. *H. shanafeltae,* new species, from Morrill County, Nebraska; referred remains from Morrill, Garden, Sheridan, Sioux, and Banner counties, Nebraska; and Shannon, Jackson, Pennington, and Washabaugh counties, South Dakota. (Lower Gering Formation or deposits equal in age.)

HOLOTYPE: Skull, mandible, and associated skeleton, U.N.S.M. 1082. Figures 34, 35, 38, 40, 43.

4. *H. densa* (Loomis), from Goshen County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; and Scotts Bluff, Banner, Sioux, and Morrill counties, Nebraska. (Upper Gering.)

HOLOTYPE: Skull and mandible, A.C. 7695. Figures 35, 39.

5. *H. extrema,* new species, from Niobrara County, Wyoming; referred remains from Niobrara County, Wyoming; and Washabaugh County, South Dakota. (Monroe Creek.)

HOLOTYPE: Skull, F:A.M. 45602. Figures 35, 38.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS, AND SYNONYMY

HADROLEPTAUCHENIA

TOTAL AVAILABLE SPECIMENS: 207[1]

1. **Hadroleptauchenia eiseleyi,**[2] new species

From oreodont faunal "Zone A" of the Brule, Scotts Bluff County, Nebraska

DESCRIPTION

SKULL: (Known from maxilla only). Slightly smaller than example of *H. eiseleyi,* geologic variety, from "Zone B" of the Brule in the same phylogenetic line.

MANDIBLE: (Known from immature specimen only).

DENTITION: P^4–M^3 shorter than in examples of *Pseudocyclopidius orellaensis* from the same faunal zone; slightly smaller than in example of *H. eiseleyi,* geologic variety.

LIMBS: (Unknown).

MEASUREMENTS: Table 13 (p. 304).

ILLUSTRATIONS: Figures 35 and 38.

DISCUSSION

The new species *H. eiseleyi* is represented by three individuals. Their importance is that they represent one of two phyla of the leptauchenins from oreodont faunal "Zone A" of the Brule Formation. It is of interest that "Zone A" has yielded more oreodonts than other Brule zones, but leptauchenin remains are rare.

Previous to this report, the leptauchenins were considered limited to oreodont faunal "Zone D" ("*Leptauchenia* beds") of the Brule and to the lower Miocene. At this time, they are known from all four zones of the Brule. Examples of this genus are known from the Brule, Gering, and Monroe Creek deposits.

[1] Includes 127 F:A.M. and 53 U.N.S.M. specimens.

[2] Named in honor of Dr. Loren C. Eiseley of the University of Pennsylvania. Dr. Eiseley spent several summers collecting fossils as a member of the University of Nebraska State Museum field party (1931–1933).

Three specimens are here recorded:

HOLOTYPE

Partial left maxilla with P^4–M^3. (w)	U.N.S.M. 28208	From oreodont faunal "Zone A" of the Brule Formation, 6 mi. E. of Lyman, North Platte drainage, Scotts Bluff County, Nebraska; collected by E. L. Blue, Frank Crabill, Loren C. Eiseley, Gordon Graham, Robert Long, Mylan Stout, Eugene Vanderpool, and Marian and Bertrand Schultz, 1933 Figures 35, 38

REFERRED FROM SCOTTS BLUFF COUNTY, NEBRASKA

FROM TYPE LOCALITY, 6 MI. E. OF LYMAN, SCOTTS BLUFF COUNTY, NEBRASKA (COLLECTED BY C. BERTRAND SCHULTZ AND ASSOCIATES, 1934):

MAXILLA		U.N.S.M.
Partial left maxilla with P^3(br.)–M^2	(w)	28465
MANDIBULAR RAMUS (IMMATURE)		
Left ramus with I_2–/C rt. and P_1–dP_2–M_2	(I)	28466

1a. Geologic Variety

From oreodont faunal "Zone B" of Brule Formation, 8 mi. N. of Rockyford, White River drainage, Shannon County, South Dakota

DISCUSSION

The maxilla listed below is of an immature individual from "Zone B" of the Brule. Its size suggests an ancestral form of *Hadroleptauchenia primitiva.* The occurrence of a leptauchenin in "Zone B" of the Brule is important, because any evidence below "Zone D" is rare. It is hoped that more complete material will be found from these lower zones.

EXAMPLE (COLLECTED BY MORRIS F. SKINNER AND ASSOCIATES, 1953)

MAXILLA

Partial left maxilla with dP^3–M^3 (germ, br.). (I) F:A.M. 45646

2. **Hadroleptauchenia primitiva,** new species

From oreodont faunal "Zone D" of the Brule Formation, Washabaugh County, South Dakota; referred remains from Washabaugh, Jackson, Shannon, and Fall River counties, South Dakota; Sioux, Scotts Bluff, and Morrill counties, Nebraska

Leptauchenia decora Leidy: SINCLAIR (in part), 1910, p. 196, fig. 1. SCOTT (in part), 1940, pp. 703–705, pl. 74, figs. 1–1B, 2–2A. THORPE (in part), 1937, p. 235, pl. 48, fig. 2.

DESCRIPTION

SKULL: Small in size, smaller than in examples of *Hadroleptauchenia shanafeltae* and *Pseudocyclopidius frankforteri,* larger than in those of *Leptauchenia decora;* mesocephalic; sagittal crest light, lighter than in examples of *H. shanafeltae;* orbit oblong (anteroposteriorly); malar below orbit shallower than in Miocene forms of genus; lacrimal fossa small but deep; muzzle compressed, more so than in examples of *H. shanafeltae;* auditory bulla inflated, smaller than in those of *H. shanafeltae.*

MANDIBLE: Ramus light and shallow, more so than in examples of *H. shanafeltae;* ascending ramus low.

DENTITION: Light, noticeably so when compared with that of examples of *H. shanafeltae;* premolars more crowded than in latter species, external superior styles less massive than in other examples of genus.

LIMBS: Light and short, more so than in examples of *H. shanafeltae.*

MEASUREMENTS: Table 13 (p. 304).

ILLUSTRATIONS: Figures 34, 35, 38, 40, 53.

DISCUSSION

Hadroleptauchenia primitiva and *Leptauchenia decora* are both reported from oreodont faunal "Zone D" of the Brule Formation. Evidently the larger species, *H. primitiva*, belonged to a faster evolving phylogenetic line than did the smaller form, *L. decora*. In *H. primitiva* the skull, when compared with that of *L. decora*, is larger but less brachycephalic, possesses larger auditory bullae, and has more hypsodont cheek teeth.

Sinclair[1] discussed material referred to *Leptauchenia* in the Princeton University Museum and considered that it included examples of both "*L. decora* and *L. nitida*." He also mentioned his restoration of a composite skeleton of *L. decora*, and stated: "The major portion of the skeleton is drawn from two individuals of *Leptauchenia decora* (Nos. 10753, 10773, Princeton University collection) supplemented occasionally by other specimens of the same species. The forefoot is from a somewhat smaller individual of *L. decora* (No. 10770) while the hind foot, with the exception of the tarsus, is enlarged to scale from *L. nitida* (No. 10765)."

Thorpe[2] accepted Sinclair's restoration as typical of *L. decora* and reported that the composite skeleton consisted of parts of three specimens, P.U. 10753, 10770, and 10773. Scott[3] also referred to Sinclair's restoration and reported: "The dimensions of the skeleton are taken from several more or less complete individuals, chiefly from Nos. 10,765 and 10,770. The former comprises two skeletons of almost exactly the same size and therefore indistinguishable, and with only one skull, which were found together."

Sinclair[1] discussed material referred to *Pepration*, using specimen P.U. 10765 as a basis, but actually considered the smaller form to be referable to *Sespia nitida*. Scott reported that P.U. 10765 consisted of two skeletons with one skull, and was the basis for much of Sinclair's measurements. The present writers, however, found that P.U. 10765 consists of two skulls, a mandible, a partial left mandibular ramus, and parts of two postcranial skeletons.

These skeletons, with specimens P.U. 10773 and 10770, appear to be referable to *L. decora*, but P.U. 10753 appears to be typical of *Hadroleptauchenia primitiva*, a larger species than *Leptauchenia decora*.

The F:A.M. specimens were collected by Morris F. Skinner and associates, 1939, 1944, 1945, 1950, 1955; and the U.N.S.M. examples, by C. Bertrand Schultz and associates, 1934, 1936, 1937, 1939, 1950, 1951.

Twenty-five specimens are here recorded:

HOLOTYPE

Skull with C/(rt.)–M³. (w+)	F:A.M. 45577	From oreodont faunal "Zone D" of Brule Formation, "*Leptauchenia* zone," Hay Creek, White River drainage, Washabaugh County, South Dakota; collected by Ralph Mefferd and Morris F. Skinner, 1939 Figures 35, 38, 53

REFERRED FROM (A) WASHABAUGH, (B) JACKSON, (C) SHANNON, AND (D) FALL RIVER COUNTIES, SOUTH DAKOTA; (E) SIOUX, (F) SCOTTS BLUFF, AND (G) MORRILL COUNTIES, NEBRASKA

A. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM 8 MI. S. AND 2 MI. W. OF INTERIOR:

SKULL		F:A.M.
Partial skull with P⁴–M³	(M+)	45585

[1] 1910, p. 196, fig. 1.
[2] 1937, pl. 48, fig. 2.
[3] 1940, p. 703.

B. FROM WHITE RIVER DRAINAGE, JACKSON COUNTY, SOUTH DAKOTA

FROM ½ MI. E. OF CEDAR PASS:

SKULL AND MANDIBLE		F:A.M.
Skull with P^1(rt.)–M^3 and mandible with I_1–I_3 rt. and /C–M_3	(w‡)	45555

C. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM SE. CORNER OF SHEEP MT.:

SKULL AND MANDIBLE		F:A.M.
Partial skull with P^1–M^3 and mandible with P_2–M_2	(w‡)	56860

C′. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA (COLLECTED BY J. B. HATCHER, 1893)

FROM CORRAL DRAW:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS		P.U.
Skull with P^2(rt.)–M^3 (P^3 br.), mandible with /C–P_3 rt. and P_4–M_3, partial scapula, partial humerus, partial radius, partial ulna, parts of femur, misc. foot bones, atlas, vertebrae (attached to skull), and fragments. Figured by Scott, 1940, pl. 75, figs. 2–2A (in part)	(–M)	10753

SKULL		
Partial skull with I^2–P^2 rt. and P^3(br.)–M^3 (M^1 br.)	(M+)	10755

FROM COTTONWOOD CREEK AREA:

SKULL AND MANDIBLE (ATTACHED)		
Skull with I^1–I^3 rt. and C/(br.)–M^3 and mandible with I_1–/C rt. and P_1(br.)–M_3	(w)	11045

The above three Princeton University specimens were referred to *Leptauchenia decora* by Scott, 1940.

D. FROM WHITE RIVER DRAINAGE, 7 MILES NORTHWEST OF SLIM BUTTE, FALL RIVER COUNTY, SOUTH DAKOTA

MANDIBLE		F:A.M.
Partial mandible with P_4(br.)–M_3	(w‡+)	56862

D′. FROM GENERAL AREA, SOUTH DAKOTA

SKULL AND MANDIBLE		U.S.N.M.
Skull with C/–M^3 (P^3 br.) and partial mandible with /C(alv.)–M_3 (P_2–P_3 alv., P_4 br.)	(w+)	2074

E. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM AREA OF U.N.S.M. COLL. LOCALITIES SX–20 AND SX–21:

SKULL		U.N.S.M.
Partial skull with M^2(alv.)–M^3	(w+)	28233

FROM U.N.S.M. COLL. LOC. SX–22:

SKULL AND MANDIBLE		
Skull with P^1(rt.)–M^3 and mandible with P_1–P_2 rt. and P_3–M_3	(M+)	28561

MANDIBULAR RAMUS		U.N.S.M.
Right ramus with /C–P_2 alv. and P_3(rt.)–M_3	(w)	28223

FROM U.N.S.M. COLL. LOC. SX–27:

SKULL AND MANDIBLE		
Fragmentary skull with dP^3–M^2 and partial mandible with dP_4(br.)–M_2	(I)	28562

FROM U.N.S.M. COLL. LOC. SX–43:

SKULL AND MANDIBLE		
Fragmentary skull with P^1–dP^2–M^2 (P^2 alv.) and partial mandible with I_1–I_3 alv. and /C–dP_2–M_3(germ)	(I)	28563

E′. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, U.N.S.M. COLL. LOC. SX–6 (=F:A.M. COLL. LOC. "10 MI. N. OF HARRISON, 2½ MI. E. OF WARBONNET CR., W. END"), SIOUX COUNTY, NEBRASKA

SKULL		F:A.M.
Partial skull with P^1(br.)–M^3	(w)	56863

F. FROM NORTH PLATTE RIVER DRAINAGE, NORTH SLOPE OF WILDCAT RIDGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM SCOTTS BLUFF MONUMENT AREA, U.N.S.M. COLL. LOC. SF–101:

2 MANDIBULAR RAMI		U.N.S.M.
Partial mandible with P_1–dP_2(br.)–M_1	(I)	28564
Partial right ramus with I_1–I_3 rt. and /C(alv.)–dP_2–M_2(br.)	(I)	28565

FROM STEAMBOAT ROCK:

SKULL		
Fragmentary skull with P^1–dP^2–M^2(erupt.)	(I)	28566

G. FROM NORTH PLATTE RIVER DRAINAGE, NORTH SIDE OF WILDCAT RIDGE, MORRILL COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. MO–111:

2 MAXILLAE		U.N.S.M.
Partial right maxilla with P^4(br.)–M^3	(w)	28568
Partial right maxilla with dP^2–M^1	(I)	28252

FROM U.N.S.M. COLL. LOC. MO–112:

SKULL		
Inferior portion of skull with I^1–dP^2–M^3(erupt.)	(I)	28567

G′. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, SOUTH SLOPE OF WILDCAT RIDGE, MORRILL COUNTY, NEBRASKA

FROM U.N.S.M. COLL. MO–104 (=F:A.M. COLL. LOC. "E. SIDE ROUNDHOUSE ROCK"):

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS		F:A.M.
Skull with C/(br.)–M^3, mandible with P_1–M_3, partial humerus, tibia, partial pes, and vertebrae	(w‡⁺)	56866
Posterior portion of skull with P^2–M^3, mandible with P_1(rt.)–M_3, and tibia	(–M)	56867

SKULL AND MANDIBULAR RAMUS		F:A.M.
Posterior portion of skull with M^2–M^3 and partial left ramus with M_1–M_2 br. and M_3	(M+)	56868

FROM U.N.S.M. COLL. LOC. MO–108:

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with P_4–M_3	(M+)	28272

3. **Hadroleptauchenia shanafeltae,**[1] new species

From lower part of Gering Formation, Morrill County, Nebraska; referred remains from Morrill, Garden, Sheridan, Sioux, and Banner counties, Nebraska; and from Gering equivalent, Shannon, Jackson, Pennington, and Washabaugh counties, South Dakota

DESCRIPTION

SKULL: Slightly larger than in examples of *H. primitiva,* smaller than in those of *H. densa;* orbit more rounded than in *H. primitiva;* malar deeper below orbit than in latter species; lacrimal fossa with less depth than in examples of *H. primitiva;* muzzle broader and more squarish than in latter species; auditory bulla inflated, but less so than in examples of *H. densa.*

MANDIBLE: Larger and deeper than in examples of *H. primitiva,* smaller than in examples of *H. densa;* inferior border of ramus with less prominent concave surface below M_3 than in latter species.

DENTITION: Heavier and broader series than in examples of *H. primitiva,* more equal to those of *H. densa.*

LIMBS: Medium in size between examples of *H. primitiva* and those of *H. densa.*

MEASUREMENTS: Tables 13 and 15 (pp. 304 and 326).

ILLUSTRATIONS: Figures 34, 35, 38, 40, 43.

DISCUSSION

The remains of *Hadroleptauchenia shanafeltae* from the lower Gering or deposits of equivalent age are well represented in the U.N.S.M. and F:A.M. collections from Nebraska and South Dakota. The remains of *Hadroleptauchenia* from the Little Muddy Creek and Horse Creek areas in Wyoming do not include *H. shanafeltae,* because the Gering deposits there represent only the upper part of this formation. Examples of *H. shanafeltae* are restricted to the lower part of the Gering, whereas those of *H. densa* are abundant in the upper portion. In the phylogenetic lines of the leptauchenins, there appear to be specific differences between the lower and upper Gering forms. In *Mesoreodon,*[1] from the material at hand, apparently phylogenetic development took place less rapidly than in the leptauchenin lines during the time of Gering forms. In *Mesoreodon,*[2] from the upper Gering are not specifically different than those derived from the lower part of the formation. The lower Gering examples of *Mesoreodon* nevertheless have a tendency to be somewhat smaller than those from the upper Gering.

Morris F. Skinner and associates collected a number of leptauchenin specimens from "above the base of the 1st white layer" at Sheep Mountain, Cedar Pass, and other critical localities in South Dakota. These specimens have proved to be of value and interest in faunal correlations. The deposits from "above the base of the 1st white layer" at Sheep Mountain yielded a large number of specimens representing the Leptaucheniinae, as well as some examples of the Promerycochoerinae and the Desmatochoerinae. The examples of *Hadroleptauchenia shanafeltae* from the lower Gering deposits of the North Platte River Valley of Nebraska are similar to those from the top of Sheep Mountain and are considered by the present writers to be the same species.

The U.N.S.M. collections (1932–1938) were made by field parties which included the following collectors: E. L. Blue, Frank W. Crabill, Frank R. Denton, Loren C. Eiseley, Gordon Graham, Robert Kubicek, Robert Long, John Mercer, Marian and Bertrand Schultz, Mylan Stout, S. R. Sweet, Lloyd G.

[1] Named in honor of Miss Marjorie Shanafelt, a staff member of the University of Nebraska State Museum, 1916–1959.

[2] Schultz and Falkenbach, 1949, p. 131.

Tanner, Harry Tourtelot, Eugene Vanderpool, Lynn Robert Wolfe, and associates. The U.N.S.M. specimens found in 1950, 1951, 1954, and 1957 were collected by John DeHaes, William Derieg, Jerry Folsom, W. D. Frankforter, Cyril Harvey, Edward F. Sabatka, C. Bertrand Schultz, Lloyd G. Tanner, Loren Toohey, and associates. The F:A.M. examples were secured by Morris F. Skinner and associates (Ralph Mefferd and Gordon Fletcher, 1938; Ralph Mefferd, 1939; and Thomas Lucas and Morris F. Skinner, Jr., 1950).

Fifty-seven specimens are here recorded:

HOLOTYPE

Skull with I^2(br.)–M^3 and mandible with P_1–M_3, associated with skeleton left in original matrix for exhibition. (w‡)	U.N.S.M. 1082	From lower part of Gering Formation, North Platte River drainage, Pumpkin Creek Valley, Roundhouse Rock, SW. of Bridgeport, U.N.S.M. Coll. Loc. MO–104, Morrill County, Nebraska; collected by Mr. and Mrs. S. R. Sweet, Bridgeport, Nebraska, 1933 Figures 34, 35, 38, 40, 43

REFERRED FROM (A) MORRILL, (B) GARDEN, (C) BANNER, (D) SIOUX, AND (E) SHERIDAN COUNTIES, NEBRASKA; (F) SHANNON, (G) PENNINGTON, (H) JACKSON, AND (I) WASHABAUGH COUNTIES, SOUTH DAKOTA

A. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, MORRILL COUNTY, NEBRASKA

From U.N.S.M. Coll. Loc. MO–103:

SKULL — U.N.S.M.

Skull with P^1–P^2 rt. and P^3–M^3 . . . . (–m) 28569

The P^3 of the above specimen has a prominent internal, posterior cusp. This is larger than in other examples, possibly owing partly to the stage of wear.

From U.N.S.M. Coll. Loc. MO–104 (=F:A.M. Coll Loc. "½ Mi. NW. of Roundhouse Rock"):

2 SKULLS AND MANDIBLES — F:A.M.

Partial skull with I^2–M^3 and mandible (attached) with P_1–M_3. . . . . (w+) 56869

U.N.S.M.

Partial skull with C/–dP^2–M^2 and partial mandible with P_1(rt.)–dP_2–M_3(germ) . . (i) 28570

SKULL

Skull with P^1(rt.)–dP^1–M^2 . . . . (i) 28571

From U.N.S.M. Coll. Loc. MO–105:

MANDIBULAR RAMUS

Partial right ramus with M_1(rt.)–M_3 . . . . (w‡) 28572

From U.N.S.M. Coll. Loc. MO–107:

2 ASSOCIATED INDIVIDUALS

Partial skull with P^1(erupt.)–dP^2–M^1 and partial left ramus with P_1–P_2 rt. and dP_3–M_1 (dP_4 alv.). . . . . (i) 28573A

Partial right and left maxillae with dC/–M^1(germ) and partial mandible with dP_2–M_1 . . . . (i) 28573B

From U.N.S.M. Coll. Loc. MO–107:

MANDIBULAR RAMUS		U.N.S.M.
Left ramus with I_1–P_2 alv. and dP_3–M_2(erupt.)	(I)	28257

FROM U.N.S.M. COLL. LOC. MO–108:

SKULL		
Inferior, anterior portion of skull with C/–dP^1–M^1	(I)	28413

FROM 4 MI. W. OF U.N.S.M. COLL. LOC. MO–108:

SKULL AND MANDIBLE (ATTACHED)		
Inferior portion of skull with dP^1–M^2 and mandible with I_1–/C rt. and P_1–dP_2–M_2	(I)	28574

A′. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM N. SIDE OF WILDCAT RIDGE, ¾ MI. N. OF U.N.S.M. COLL. LOC. MO–108:

SKULL		U.N.S.M.
Inferior, anterior portion of skull with P^1(alv.)–M^3	(M+)	28575

FROM 6 MI. E. AND S. OF BROADWATER, U.N.S.M. COLL. LOC. MO–111:

SKULL AND MANDIBLE		
Fragmentary skull with P^2(br.)–M^3 and partial mandible with M_3(br.)	(M+)	28576
MANDIBULAR RAMUS		
Partial right ramus with P_3(alv.)–M_3	(W+)	28214

B. FROM NORTH PLATTE RIVER DRAINAGE, BLUE CREEK VALLEY, NORTHWEST OF LEWELLEN, GARDEN COUNTY, NEBRASKA (COLLECTED BY T. MYLAN STOUT, 1931–1932)

3 MAXILLAE		U.N.S.M.
Partial maxilla with P^2–M^3	(M+)	28458
Partial maxilla with P^1–P^2 rt. P^3–M^3	(W‡‡)	28459
Partial left maxilla with P^4–M^2	(W)	28460
5 MANDIBULAR RAMI		
Partial right ramus with M_1–M_3(br.)	(W+)	28461
4 partial left rami with		
P_1(alv.)–M_3 (M_1 absent)	(M+)	28453
P_1–P_4 br. and M_1–M_3(br.)	(W‡)	28462
P_1–P_2 rt. and P_3–M_3.	(M)	28463
dP_4(br.)–M_2(erupt.)	(I)	28464

C. FROM NORTH PLATTE RIVER DRAINAGE, NORTH SLOPE OF WILDCAT RIDGE, BANNER COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. BN–102:

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with P_4–M_3	(W+)	28581

C′. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, BANNER COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. BN–101:

SKULL AND MANDIBLE		U.N.S.M.
Partial skull with P^2–M^3 and mandible with P_1–P_3 alv. and P_4–M_3 (M_1 br.)	(w)	28582

FROM 2 MI. E. OF HUBBARD GAP:

MANDIBULAR RAMUS		
Partial right ramus with P_1–M_3	(w+)	28228

FROM S. SIDE OF HUBBARD GAP:

SKULL		
Inferior, anterior portion of skull with P^1–dP^2–M^2	(I)	28431

FROM 1 MI. E. OF WRIGHT'S GAP:

MANDIBLE		
Partial mandible with I_1–I_3 alv. and /C–M_3	(w)	28583

D. FROM WHITE RIVER DRAINAGE, PINE RIDGE AREA, U.N.S.M. COLL. LOC. SX–22, SIOUX COUNTY, NEBRASKA

2 ASSOCIATED INDIVIDUALS		U.N.S.M.
Partial skull with C/(rt.)–M^3 and mandible with P_1–P_2 br. and P_3–M_3	(w‡)	28578A
Partial left maxilla with dP^1–M^2	(I)	28578B
SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with C/–M^3, mandible with P_1–M_3, partial humerus, vertebrae, and ribs	(w‡+)	28579
SKULL		
Skull with I^1–I^2 rt. and I^3–M^3	(w+)	28580

E. FROM WHITE RIVER DRAINAGE, PINE RIDGE AREA, NORTH OF RUSHVILLE, SHERIDAN COUNTY, NEBRASKA

MANDIBLE		U.N.S.M.
Partial mandible with dP_3(br.)–M_3(erupt.)	(I)	28577

F. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

FROM SE. CORNER OF SHEEP MT., 12′–45′ ABOVE FIRST WHITE LAYER[1]:

4 ASSOCIATED INDIVIDUALS		F:A.M.
Posterior portion of skull with M^1–M^3 and mandible with P_1–M_1 br. and M_2–M_3	(w+)	56820A
Right maxilla with M^1–M^3 and partial right ramus with M_2(br.)–M_3	(w‡)	56820B
Right maxilla with dP^3–M^1	(I)	56820C
Partial right ramus with P_1–P_4 alv. and M_1(br.)–M_3	(w+)	56820D
2 ASSOCIATED INDIVIDUALS		
Fragments of skull with P^3–M^3(br.) and mandible with /C–M_3	(w)	56870A
Partial right ramus with P_3(br.)–M_3	(–M)	56870B
SKULL, MANDIBLE, AND SKELETAL ELEMENTS		
Skull with I^2–M^3 (P^1 alv.), mandible with I_3–M_3 (P_1 br.), partial humerus, partial ulna, partial manus, and fragments	(w+)	57138

[1] The exact footage above the "first white layer" is recorded in the F:A.M. catalogue for each specimen, but the examples from 12′ to 45′ above this layer at Sheep Mt. are typical of *H. shanafeltae*. Therefore, the examples are grouped together under one heading. This method of listing specimens is used throughout the present report. (See discussion, p. 423.)

2 SKULLS AND MANDIBULAR RAMI		F:A.M.
Partial skull with P^3–M^3 and mandible with P_3–M_3	(M+)	56871
Partial skull with P^2–M^3 and partial left ramus with M_1(br.)–M_3	(W)	56872

SKULL AND SKELETAL ELEMENTS

Skull with I^2–I^3 alv. and C/–M^3, and partial humerus	(W‡)	57137

5 SKULLS

5 partial skulls with		
P^3–M^3	(M+)	56873
P^3(br.)–M^3	(W‡)	56874
P^1(alv.)–M^3	(M+)	56875
C/–M^3	(M+)	56876
C/(erupt.)–dP^2–M^1 (dP^1 br.)	(I)	56877

FROM S. END OF SHEEP MT., 20′–70′ ABOVE BASE OF FIRST WHITE LAYER, S. OF SCHOOL OF MINES CANYON:

2 SKULLS AND MANDIBLES (ATTACHED)

Partial skull with P^2–M^3 (M^1 alv.) and mandible with P_1–M_3	(W‡‡)	56878
Inferior, anterior portion of skull with P^2(rt.)–M^3 and partial mandible with I_1–P_2 alv. and P_3–M_3	(W+)	56879

SKULL

Partial skull with C/–M^3	(W‡⁺)	56880

MAXILLA

Partial right maxilla with C/(rt.)–M^3	(W‡)	56881

FROM 8 MI. E. OF ROCKYFORD:

SKULL AND MANDIBLE (ATTACHED)

Skull with C/–P^2 rt. and P^3–M^3 and mandible with I_1–/C rt. and P_1–M_3	(W+)	45579

The field record with above specimen indicates "upper part of *Leptauchenia* beds," but at the time it was collected some of the lower Miocene deposits were included in the "*Leptauchenia* beds." The specimen is similar to examples of this species from the lower part of the Gering Formation (or Sharps Formation of South Dakota). The fossilization is similar, and the matrix on this specimen is also similar to that adhering to Leidy's examples of *Pseudocyclopidius major* from South Dakota (see pp. 332 and 333). The latter species is typical of the lower Gering.

G. FROM WHITE RIVER DRAINAGE, SOUTHEAST CORNER OF PINNACLES, PENNINGTON COUNTY, SOUTH DAKOTA

3 ASSOCIATED INDIVIDUALS		F:A.M.
Fragmentary skull with dP^1–dP^4 br. and M^1–M^2 and left ramus with /C–dP_4–M_2	(I)	56883A
Partial skull with P^1(rt.)–M^3 (P^4–M^2 absent)	(W‡‡)	56883B
Partial mandible with P_1(rt.)–M_3	(W+)	56883C

The mandible is the only specimen that can be readily identified as to species.

SKULL

Partial skull with C/(rt.)–M^3	(W+)	56884

H. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA, JACKSON COUNTY, SOUTH DAKOTA

FROM CHANNEL DEPOSITS CAPPING "*Leptauchenia* BEDS" AT CEDAR PASS:

	MAXILLA		F:A.M.
Partial right maxilla with P^4(rt.)–M^3 (M^1 br.)	. . . .	(w)	56882

FROM NEAR CEDAR PASS:

	SKULL AND MANDIBLE		
Skull with I^2–I^3 rt. and C/–M^3 and mandible with I_1(rt.)–M_3		(M+)	45572

This specimen is tentatively referred to this species.

I. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM 1MI. NW. OF QUIVER HILL:

	MAXILLA AND MANDIBULAR RAMUS		F:A.M.
Partial right maxilla with P^4–M^3 and partial left ramus with M_2–M_3.		(w)	56885

FROM E. SIDE OF POTATO CREEK:

	SKULL AND MANDIBLE (ATTACHED)		
Partial skull with P^1(br.)–M^3 and mandible wtih I_1–P_1 rt. and P_2–M_3		(w)	45566

4. **Hadroleptauchenia densa** (Loomis)

From upper part of Gering Formation, Niobrara County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; Scotts Bluff, Banner, Sioux and Morrill counties, Nebraska

Leptauchenia densa LOOMIS, 1925a, p. 245, figs. 3, 4.

Cyclopidius densa (Loomis): SCHLAIKJER, 1935, p. 161, pls. 24, 25.

Cyclopidius densus (Loomis): THORPE, 1937, p. 243, figs. 170, 171 (fig. 172 and pl. 49 are not this species; see p. 336, this report).

CHARACTERS

SKULL: Larger than in examples of *H. shanafeltae* slightly smaller than in those of *H. extrema;* sagittal crest slightly higher than in those of *H. shanafeltae;* lacrimal fossa less deep than in latter species.

MANDIBLE: Same size comparison as skull.

DENTITION: Series average longer than examples of *H. shanafeltae;* within range of those of *H. extrema.*

LIMBS: (Unknown).

MEASUREMENTS: Table 13 (p. 304).

ILLUSTRATIONS: Figures 35, 39, 53, 55.

DISCUSSION

Examples of *Hadroleptauchenia densa* and those of *H. extrema* differ mostly in that the latter have an elongated posterior portion. The dentition apparently is within the same size range. It is of interest that there is more apparent size change between examples of *H. shanafeltae* from the lower Gering and those of *H. densa* from the upper Gering than between the latter and those of *H. extrema* from the Monroe Creek.

In the same report with the description of *"Leptauchenia"* (= *H. densa*), Loomis[1] also discussed *"Cyclopidius"* (= *Pseudoleptauchenia*) *lullianus* and stated, ". . . the skeleton of *Cyclopidius* [*lullianus*] (Fig. 1), [was] found in the Lower Rosebud, 25 miles south of Torrington, Wyo." This presumably is the Horse Creek area that includes 66 and Bear Mountains. Under the species *densa* Loomis[2] included specimens that came from ". . . the south side of Goshen Hole." This would indicate that the locality is the same Horse Creek area as worked by F:A.M. field parties, which is here considered as containing upper Gering deposits. (See discussion of these localities under *P. lullianus*, p. 336.)

Thorpe[3] unintentionally referred Loomis' specimens, which were shown in figures 1 and 2, to *H. densa.* Loomis' figures actually illustrate *P. lullianus,* and the captions identify the skeleton and front foot as *"Cyclopidius lullianus."* Thorpe did retain the correct specimen number for the holotype of *H. densa.*

Loomis, in describing *"Leptauchenia densa,"* considered "some 20 specimens from both Muddy Creek, . . . and from the south side of

[1] 1925a, p. 242.
[2] 1925a, p. 245.
[3] 1937, p. 243, fig. 172, pl. 49, fig. 1.

Goshen Hole, both localities in Wyoming." It is known that the holotype came from the Muddy Creek area, which contains deposits of both Gering and Monroe Creek (see discussion under *P. lullianus*, p. 336). The balance of the specimens were not identified by numbers, and thus some may be referable to the species *densa* and others to *lullianus*.

Schlaikjer,[1] in his report on the Goshen Hole, referred several individuals to *"Cyclopidius densa"* and concluded that the specimens were from the Harrison Formation. In fact, Schlaikjer considered all the deposits in the particular portion of Goshen Hole above the Brule as Harrison Formation. The present writers consider these same deposits as Gering in age. The geology of this area was discussed under the Promerycochoerinae and the Desmatochoerinae.

Thorpe[2] considered the holotype of *H. densa* as coming from deposits equal to "lower Rosebud." Loomis also considered that the specimen came from the "lower Rosebud" and concluded that these particular deposits were not the same age as those of the "Lower Harrison."

Loomis, Schlaikjer, and Thorpe all discussed the presence or absence of three superior incisors. There are definite examples with just two superior incisors, as demonstrated in F:A.M. 56892. Perhaps only a trend to lose the third incisor is indicated. From the evidence at hand, which is not conclusive because many examples lack the premaxilla region, the earlier (Oligocene) forms had three incisors and the Miocene forms only two, i.e., within the Leptaucheniini. In the Sespiini, however, the three incisors apparently are present in specimens from the Miocene. As mentioned previously, all examples of lower dentition possess three incisors.

Schlaikjer's "phylogenetic chart" indicates that he concluded that the beds above the Brule in the Goshen Hole were of Harrison age. Also he considered that the three so-called "Harrison" species, *simus, densa,* and *lullianus,* were in a direct phylogenetic sequence within the genus *Cyclopidius.* The present writers consider the three species in question to be members of three different phyla: *Cyclopidius simus, Hadroleptauchenia densa,* and *Pseudocyclopidius lullianus*—all from the Gering or deposits equal in age.

As noted above in this report, no leptauchenins are known from above the Monroe Creek deposits or its equivalent in age. Thorpe[3] described *Cyclopidius (Chelonocephalus) schucherti* and gave its geologic occurrence as "Sheep Creek," but the present writers have referred this form to *Leptauchenia decora* from "Zone D" of the Brule. (See discussion, p. 000.)

It should be noted that both the Frick Laboratory and the University of Nebraska State Museum have large collections from the Harrison and Marsland formations, but no leptauchenins have ever been found in these deposits. Also the Frick Laboratory and the American Museum of Natural History have large collections from the Sheep Creek Formation which also lacks examples of leptauchenins.

The F:A.M. specimens from Wyoming and Pumpkin Creek valley, Nebraska, were collected by J. C. Blick, Everett De Groot, Gene Roll, Charles H. Falkenbach, Nelson J. Vaughn, and associates, 1932–1944; and those from the North Platte River valley, Nebraska, by Morris F. Skinner and associates, 1942, 1955. The U.N.S.M. collection was made by C. Bertrand Schultz and associates, 1933-1938.

Ninety-seven specimens are here recorded:

HOLOTYPE

Partial skull with I^2alv.–M^3 (erupt.) and mandibular ramus[4] with P_1–dP_4–M_2(br.). (M+)	A.C. 7695	From upper part of Gering Formation, "Goshen Hole," Horse Creek basin, North Platte River drainage, Goshen County, Wyoming; collected by F. B. Loomis, 1922 Figured by Loomis, 1925a, figs. 3–4; Thorpe, 1937, figs. 170–171 This paper, figures 35, 39

[1] 1935, pp. 161, 163, 167, and 168.
[2] 1937, p. 243.
[3] 1921b, p. 415; 193, p. 256.
[4] It should be noted that the permanent P^4 is present in the skull, but dP_4 is present in the ramus.

REFERRED FROM (A) NIOBRARA, (B) GOSHEN, AND (C) LARAMIE COUNTIES, WYOMING; (D) SCOTTS BLUFF, (E) BANNER, (F) SIOUX, AND (G) MORRILL COUNTIES, NEBRASKA

A. FROM NORTH PLATTE RIVER DRAINAGE, NIOBRARA COUNTY, WYOMING

From Little Muddy Creek:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS, IMMATURE

		F:A.M.
Partial skull with dP^2(br.)–M^2, mandible with P_1–P_2 rt. and dP_3–M_3(germ), 2 humeri (1 partial), 2 radii (1 partial), 2 ulnae (1 partial), partial manus, 2 femora (1 partial), 2 tibiae (1 partial), partial pes, pelvis, vertebrae, and ribs	(I)	56886

2 SKULLS AND MANDIBLES (ATTACHED)

Inferior, anterior portion of skull with P^1–M^1 br. and M^1–M^2 and mandible with I_1–M_1 br. and I_2–M_3	(W)	56887
Fragmentary skull with dP^4–M^2 and partial mandible with M_1–M_2	(I)	56888

SKULL AND MANDIBULAR RAMI

Inferior, anterior portion of skull with C/–dP^2–M^2 and ramus with I_2–I_3 rt. and /C–dP_2–M_2	(I)	56889

13 SKULLS

13 partial skulls with		
C/(rt.)–M^3	(W)	45634
Field data on this specimen are not known; however, it was obtained at a time when collecting was concentrated at Little Muddy Creek.		
P^1–dP^2–M^2	(I)	56890
C/–dP^1–M^2	(I)	56891
I^2–dP^2–M^2 (I^2 rt.)	(I)	56892
I^2(br.)–dP^2–M^2	(I)	56893
C/(erupt.)–dP^1–M^2(germ)	(I)	56894
I^2–M^3	(W‡)	56895
I^3–M^3 (P^1 rt.)	(M+)	56896
P^3–M^3	(W‡⁺)	56897
C/–M^3(br.)	(W+)	56898
I^2(br.)–dP^2–M^2(erupt.)	(I)	56899
C/–dP^1–M^1	(I)	56900
C/–dP^2–M^2	(I)	57157

4 ASSOCIATED MAXILLAE AND MANDIBULAR RAMI

Right and left maxillae with P^3–M^3 and partial mandible with P_2–M_3. Figure 53	(W+)	56901A
Partial right maxilla with dP^3(alv.)–M^2 and partial right ramus with dP_3–M_1 (dP_4 br.)	(I)	56901B
Partial left maxilla with P^4–M^3	(W+)	56901C
Partial left ramus with P_1(alv.)–dP_3–M_2 (P_1 rt.)	(I)	56901D

MAXILLA AND MANDIBLE

Partial right maxilla with dP^4–M^1 and partial mandible with P_1, dP_4(br.)–M_3(br.)	(I)	57156

14 MAXILLAE

Right and left maxillae with P^3–M^3	(M)	56902
9 partial right maxillae with		
dP^4–M^2	(I)	56903
dP^4–M^2	(I)	56904
M^1–M^2	(W)	56905
M^1(br.)–M^3	(W‡⁺)	56906

		F:A.M.
P^1–dP^2–dP^4	(i)	56907
C/–P^1–dP^2–M^1	(i)	56908
P^1–dP^2–M^1	(i)	56909
dP^3–M^2(br.)	(i)	56910
C/(rt.)–dP^2–M^1	(i)	56911
5 partial left maxillae with		
P^4–M^3	(w)	56912
P^1–dP^2 rt. and dP^3–M^1	(i)	56913
P^4–M^2	(w+)	56914
dP^4–M^2	(i)	56915
C/–dP^2–M^2(erupt.)	(i)	56916

10 MANDIBLES

10 partial mandibles with		
P_1–P_3 rt. and P_4–M_3	(m+)	56917
I_1–M_3	(w‡)	56918
I_1–M_3(erupt.)	(−m)	56919
I_3–/C rt. and P_1–M_3	(w+)	56920
I_1–dP_2–M_2(P_1 rt.)	(i)	56921
dP_2(br.)–M_2 (P_4 erupt.)	(i)	56922
I_1–P_1 rt. and P_2–M_3	(w)	56923
dP_2(br.)–M_2(br.)	(i)	56924
P_1(rt.)–dP_2–M_2	(i)	56925
/C–dP_2–M_2	(i)	56926

17 MANDIBULAR RAMI

4 partial right rami with		
M_1–M_3	(w+)	56927
I_2(rt.)–M_3	(w+)	56928
dP_2–M_1	(i)	56929
P_1–P_2 rt. and dP_3–M_2	(i)	56931
13 partial left rami with		
P_4–M_3	(−m)	56932
P_3(br.)–M_3	(w+)	56933
dP_3(br.)–M_2	(i)	56934
dP_4–M_2	(i)	56935
M_1–M_3 (M_1–M_2 br.)	(m+)	56936
dP_4–M_2(erupt.)	(i)	56937
M_3	(w+)	56938
P_1–M_3	(w)	56939
M_2(br.)–M_3	(w‡+)	56940
P_1(rt.)–dP_3–M_1 (P_2 alv.)	(i)	56941
P_1–dP_2–M_1	(i)	56942
dP_4–M_1	(i)	56943
P_1–P_2 rt. and dP_3–M_1	(i)	56944

FROM MUDDY CREEK, 5 MI. NE. OF BRIDGE (GERING FORMATION):

SKULL AND MANDIBULAR RAMUS

Skull with C/–M^3 and left ramus with P_3–M_3. Figures 34, 35, 38, 40	(w)	37525

FROM 2 MI. SW. OF FLATTOP:

SKULL

Inferior, anterior portion of skull with C/(br.)–M^2	(w)	56945

MANDIBULAR RAMUS

Partial left ramus with dP_3–M_3(germ)	(i)	56946

B. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, GOSHEN COUNTY, WYOMING

FROM W. END OF SOUTH SIDE OF 66 MT.:

		F:A.M.
SKULL AND MANDIBLE (ATTACHED)		
Partial skull with C/–M^3 and mandible with I_1–M_3	(W)	56947
SKULL		
Partial skull with P^1–M^3	(W+)	56948
MANDIBULAR RAMUS		
Partial right ramus with /C–P_3 alv. and P_4–M_3	(W‡)	56949

FROM GOSHEN COUNTY (COLLECTED BY ERICH SCHLAIKJER AND PARTY, 1931–1933):

		M.C.Z.
Skull	(M)	2850
Skull	(M)	2866
Skull	(I)	2876
Skull	(I)	2877
Anterior, inferior portion of skull		2067
Anterior, inferior portion of skull		2851

The above material was listed by Schlaikjer, 1935, p. 161.

C. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN,[1] TREMAIN AREA, LARAMIE COUNTY, WYOMING

FROM E. OF U. S. HIGHWAY NO. 85 AND S. OF HORSE CREEK:

		F:A.M.
SKULL AND MANDIBLE		
Partial skull with M^2(br.)–M^3(erupt.) and mandible with M_1–M_2	(–M)	56950

FROM TREMAIN AREA:

2 SKULLS AND MANDIBLES		
Partial skull with C/–dP^2–M^2 and partial mandible with P_1–dP_2–M_2.	(I)	56812
The above specimen has been sectioned lengthwise for an examination of the nasal-facial vacuity and the bulla region.		
Fragmentary skull with M^1–M^3 and partial mandible with M_1–M_3	(M)	56951
2 PARTIAL SKULLS		
Partial skull with M^1–M^2	(M+)	56952
Left side of skull with I^2–dP^2–M^1	(I)	56953
MAXILLA AND MANDIBULAR RAMUS		
Partial right maxilla with P^2–M^3 (M^1 absent) and partial right ramus with P_4–M_3	(M+)	56954
MANDIBLE		
Partial mandible with /C–dP_2–M_2	(I)	56955
2 MANDIBULAR RAMI		
Partial right ramus with P_2(alv.)–dP_3–M_2	(I)	57159
Partial left ramus with P_4(rt.)–M_3	(W+)	57158

[1] It should be noted that the 66 Mt. and Bear Mt. localities, and the Tremain area, are in the Horse Creek drainage, but in different counties.

D. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, SCOTTS BLUFF COUNTY, NEBRASKA

FROM 5 MI. N. AND W. OF HOGBACK MT.:

SKULL		U.N.S.M.
Skull with C/–M^3 (P^1 alv.)	(–M)	28400

FROM CASTLE ROCK, 6 MI. S. AND 3 MI. E. OF MINATARE:

MANDIBULAR RAMUS		
Partial left ramus with dP_4(br.)–M_3(br.)	(I)	28244

E. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, BANNER COUNTY, NEBRASKA

FROM S. SIDE OF 66 MT.:

MAXILLA		F:A.M.
Partial right maxilla with P^1–dP^2–M^1	(I)	56956

FROM 1 MI. E. OF WRIGHT'S GAP:

MAXILLA		U.N.S.M.
Partial left maxilla with M^1(br.)–M^3	(w‡‡)	28584

F. FROM NORTH PLATTE RIVER DRAINAGE, 2½ MILES NORTHWEST OF LAKE ALICE, SIOUX COUNTY, NEBRASKA

2 ASSOCIATED INDIVIDUALS		F:A.M.
Skull with C/–M^3 and mandible (attached) with /C–M_3	(w)	56957A
Partial skull with dP^4(br.)–M^2 and partial mandible with dP_4(br.)–M_2	(I)	56957B
2 humeri, 2 radii (1 partial), 2 ulnae (1 partial), vertebrae, and ribs		56957A–B

The above material was found associated in the field. Morris F. Skinner, the collector of the specimens, questioned the geologic occurrence as "Lower part of the Monroe Creek Formation?" The material compares readily with examples of this species from the upper part of the Gering.

SKULL AND MANDIBLE		
Partial skull with dP^4(br.)–M^2 and mandible (attached) with M_1–M_2	(I)	56958

G. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, MORRILL COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. MO–104 (=ALL F:A.M. SPECIFIC COLLECTING LOCALITIES IN VICINITY OF ROUNDHOUSE ROCK):

SKULL		F:A.M.
Skull with C/–M^3. Figure 55	(w+)	56959

FROM VICINITY OF U.N.S.M. COLL. LOC. MO–104:

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with P_1–P_3 alv. and P_4–M_3	(w‡⁺)	28585

G′. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM NORTH SLOPE OF WILDCAT RIDGE, 2 MI. NW. OF U.N.S.M. COLL. LOC. MO–108:

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with dP_4–M_2	(I)	28586

FROM 5 MI. E. AND S. OF BROADWATER, NW. OF U.N.S.M. COLL. LOC. MO–111:

MANDIBULAR RAMUS		
Partial right ramus with M_1–M_3	(w+)	28213

5. **Hadroleptauchenia extrema**,[1] new species

From Monroe Creek Formation, Niobrara County, Wyoming; referred specimens from Niobrara and Converse counties, Wyoming; and Washabaugh County, South Dakota

Description

Skull: Average length longer than in examples of *H. densa* (actually the skull is elongated posteriorly compared with those of *H. densa*); sagittal crest with tendency to be higher than those of *H. densa*.

Mandible: Same size comparison as skull.

Dentition: Series within size range of that of *H. densa*; tendency for external styles of superior molars to be more prominent than those of mentioned species.

Limbs: (Unknown).

Measurements: Table 13 (p. 304).

Illustrations: Figures 34, 35, 38, 40.

Discussion

Remains of *Hadroleptauchenia extrema* represent the last-known species of the genus in geologic occurrence. It does not differ greatly from *H. densa* from the upper part of the Gering Formation. The most outstanding difference between the two forms is the elongation of the posterior portion of the skull of *H. extrema*.

The F:A.M. specimens from Wyoming were collected by J. C. Blick, Everett DeGroot, Gene Roll, Nelson J. Vaughn, Charles H. Falkenbach, and associates, 1933–1944; and the F:A.M. examples from South Dakota, by Morris F. Skinner and associates, 1950.

Nineteen specimens are here recorded:

HOLOTYPE

Skull with C/(rt.)–M^3. (w‡) F:A.M. 45602 From Monroe Creek Formation, Muddy Creek, North Platte River drainage, Niobrara County, Wyoming; collected by John Lynch, Everett De Groot, and Charles H. Falkenbach, 1933
Figures 35, 38

REFERRED FROM (A) NIOBRARA AND (B) CONVERSE COUNTIES, WYOMING; AND (C) WASHABAUGH COUNTY, SOUTH DAKOTA

A. FROM MUDDY CREEK AREA, NIOBRARA COUNTY, WYOMING

		F:A.M.
Skull and mandible		
Inferior, anterior portion of skull with I^2–M^3 and mandible with I_1–M_3	(w)	56961
2 skulls		
Inferior, anterior portion of skull with P^1–M^3	(w‡+)	56962
Partial skull with P^1(br.)–M^3	(w‡+)	56963
Maxilla and mandibular ramus		
Partial left maxilla with P^3–M^2 and partial left ramus with P_4–M_2	(w+)	56964
2 maxillae		
Partial right maxilla with M^1–M^3	(w+)	56965
Partial right maxilla with M^1(br.)–M^3	(w‡)	56966
9 mandibular rami		
Mandible with I_1(rt.)–M_3. Figures 34, 40	(w+)	45636
Partial mandible with I_2–M_2	(w)	56930
7 partial right rami with		
M_1(br.)–M_3	(w+)	56967
P_4–M_1(br.)	(w+)	56968

[1] The name refers to the last species in the *Hadroleptauchenia* phylogenetic line.

		F:A.M.
P_4–M_3(rt.)	(w‡)	56969
P_2(rt.)–M_3(br.)	(–M)	56970
I_1–P_2 rt. and P_3–M_1	(w+)	56971
M_1–M_2	(M+)	56972
I_1–M_3	(w)	56973

B. FROM 3 MILES SOUTH OF DOUGLAS, CONVERSE COUNTY, WYOMING

MANDIBLE (IMMATURE)		F:A.M.
Partial mandible with /C–P_1–dP_2–M_2	(I)	56974

C. FROM WHITE RIVER DRAINAGE, 1 MILE WEST OF QUIVER HILL, TOP OF SECOND WHITE ZONE, 168 FEET ABOVE FIRST WHITE ZONE, WASHABAUGH COUNTY, SOUTH DAKOTA

2 MANDIBULAR RAMI		F:A.M.
Partial right ramus with I_3–P_4 rt. and M_1–M_3	(w)	56975
Partial right ramus with M_1–M_3	(w)	56976

VII. PSEUDOCYCLOPIDIUS, NEW GENUS

GENOTYPE: *Pseudocyclopidius major* (Leidy).

DESCRIPTION

SKULL: Small to medium size[1]; basal lengths ranging from 121 to 124 mm.; widths from 95 to 103.5 mm.; dolichocephalic (*P. orellaensis* from "Zone A" of Brule) to brachycephalic; moderately high to low, tendency to become lower or compressed in lower Miocene examples; sagittal crest moderately prominent to prominent; frontals wide; nasals with slight anterior projection beyond incisors; orbit small, larger than in examples of *Hadroleptauchenia,* looking outward and slightly upward and forward; malar deep below orbit; zygomatic arch with superior border approaching a wide U shape (less noticeable in examples from later geologic zones); infraorbital foramen above P^3; lacrimal fossa shallow, slightly deeper and larger than in examples of *Hadroleptauchenia*; nasal-facial vacuity extending posteriorly to a point above anterior to posterior portion of M^3 (Oligocene examples with less posterior extension); prominent depression or pit on face above premolars; auditory bullae greatly inflated, tendency to be elongated anteroposteriorly.

MANDIBLE: Moderately light to moderately robust; postsymphysis below P_4 to M_1; mandibular ramus moderately shallow to deep; inferior border of ramus with slight downward slope to a point below M_3, then a slight concave notch; ascending ramus from sub-high to high.

DENTITION: Subhypsodont (more hypsodont than in *Hadroleptauchenia*); dental formula, I^{2-3}_3, C/C, P^4_4, M^3_3; premolars not crowded; external styles of superior molars prominent, moderately massive, more so than in *Hadroleptauchenia*; tendency for premolar series to be longer than in examples of *Hadroleptauchenia.*

LIMBS: Long and massive compared with those of *Hadroleptauchenia.*

MEASUREMENTS: Tables 14 and 15 (pp. 324 and 326).

ILLUSTRATIONS: Figures 36–40, 53 (skull, mandibular rami), and 43 (limbs).

DISCUSSION

Remains of *Pseudocyclopidius* comprise the largest-skulled phylum of the leptauchenins, and are known from oreodont faunal "Zone A" of the Brule. Previous to this report, the leptauchenins were restricted in the Oligocene to "Zone D" of the Brule. *Pseudocyclopidius orellaensis* from "Zone A" is one of the first-recorded oreodonts with an inflated bulla from "Zone A." It is noteworthy that the leptauchenins possessed a well-inflated bulla throughout their phylogenetic history (including the occurrence in "Zone A"); the examples of the Miniochoerinae retained a small (minute) bulla

[1] Skulls of the *Pseudocyclopidius* line are noticeably larger than those of the *Hadroleptauchenia* line, if the specimens are obtained from the same geologic deposits.

TABLE 14

Pseudocyclopidius, New Genus. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*P. orellaensis*, new species	*P. frankforteri*, new species	*P. major*[b] (Leidy)		*P. lullianus*[c] (Thorpe)		*P. lullianus expiratus*, new subspecies
	Holotype F:A.M. 45528	Holotype F:A.M. 45500	Referred[b] U.N.S.M. 1080 (male example)	Referred U.N.S.M. 1081 (female example)	Holotype Y.P.M. 10117	Referred F:A.M. 45597	Holotype F:A.M. 45598
Stage of wear of teeth	(I)	(w‡+)	(w‡+)	(w‡)	(w)	(w‡+)	(w‡+)
Length (incl. supraoccipital crest and incisors)	(100)	(128)	138	146	—	155	—
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	(93)	115	121	124	133	((133))	((135))
Width (max.)	(56)	93.5	103.5	95	(101)	113	108
Width of brain case (max.)	25	38	44.5	41	—	45	41
Width, interorbital (min.)	(22)	43	48	48	((49))	54	61
Distance from anterior rim of orbit to anterior base of C/	40	45	47.5	46	(56)	56	((57))
Distance from anterior rim of orbit to supraoccipital crest	(59)	91	98	101	—	110	—
Width of muzzle at infraorbital foramina	26	38	40	39	(50)	50	54
Width across canines	(13)	(25)	26.5	(26)	(31)	26	—
Length, C/–M^3 incl.	—[c]	(65)	75.5	(74)	79	74	—
Length, P^1–M^3 incl.	—[c]	57	66.5	65	69	64	71
Length, P^1–P^4 incl.	28	25	28.5	28	28	27	28
Length, M^1–M^3 incl.	—[c]	33	39	40	44	49.5	44
Width of M^3 (max.)	—	14.5	16.5	17	15	16	18.5
Depth of malar below orbit	10	—	22	21	—	27	23.5

TABLE 14—(*Continued*)

MANDIBULAR RAMUS	*P. orellaensis*, new species	*P. frankforteri*, new species	*P. major* (Leidy)		*P. lullianus* (Thorpe)		*P. lullianus expiratus*, new subspecies
	Holotype F:A.M. 45528	Holotype F:A.M. 45500	Referred[b] U.N.S.M. 1080 (male example)	Referred U.N.S.M. 1081 (female example)	Holotype Y.P.M. 10117	Referred F:A.M. 34484	Holotype F:A.M. 45598
Stage of wear of teeth. . .						(w‡)	
Length (max., incl. incisors)	—	((110))	((125))	123	(132)	—	—
Length, /C-condyle incl.. .	—	102		107	122	126.5	—
Depth of jaw under coronoid	—	59	73.5	71	—	—	86
Depth of jaw below anterior edge of M_3	—	27	31	31	—	35	38.5
Length, /C–M_3 incl. . . .	—	(67)	—	79	(78)	80	—
Length, P_1–M_3 incl. . . .	—	62	((70))	73	(71)	74	75
Length, P_1–P_4 incl.	—	23	(26)	28	27	27	25
Length, M_1–M_3 incl. . . .	—	39	45	40	48	47	50

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

[b] The only measurements of the holotype (w‡) of *P. major* (A.N.S.P. 1094) are as follows: length, C/–M^3 incl., 75.5; P^1–M^3 incl., 58; P^1–M^4 incl., 28; M^1–M^3 incl., 41; width of M^3 (max.), 15.5.

[c] The only measurements of the holotype (w) of *P. quadratus* (Koerner) (Y.P.M. 13960) are as follows: P^1–P^4 incl., 27.5; M^1–M^2 incl., 28.

TABLE 15

Sespia STOCK; *Megasespia*,[a] NEW GENUS; *Leptauchenia* LEIDY; *Hadroleptauchenia*, NEW GENUS; AND *Pseudocyclopidius*, NEW GENUS. MEASUREMENTS[b] OF SKELETAL ELEMENTS

	S. marianae, new species	*S. nitida* (Leidy)	*Leptauchenia decora* Leidy	*H. shanafeltae*, new species	*Pseudocyclopidius major* Leidy		*Pseudocyclopidius lullianus* new species
	Holotype U.N.S.M. 28420A	Referred F:A.M. 45622	Referred F:A.M. 45565	Holotype U.N.S.M. 1082	Referred U.N.S.M. 1080 (♂ example)	Referred U.N.S.M. 1081 (♀ example)	Referred F:A.M. 57090
Length of humerus (articular)	68	68.5	75	84	98	96	116
Length of radius (articular)	(57)	60	—	—	76	77	87
Length of ulna (max.)	((80))	78	—	—	—	103	115
Length of metacarpal III (max.)	25.5	26.5	—	34	—	35	40.5
Length of femur (articular)	69	66	—	—	99	101	116
Length of tibia (articular)	70	69	—	—	83	83	95
Length of calcaneum (max.)	20.5	21.5	—	—	32.5	33.5	33.5
Length of metatarsal III (max.)	30	32.5	—	35	—	36.5	43

[a] The only available skeletal element of *Megasespia middleswarti* is a metatarsal III, which measures 36.5 mm.
[b] ( ), Approximate; (( )), estimated. All measurements in millimeters.

throughout their geologic history from Chadron through "Zone D" of the Brule; and the Merycoidodontinae possessed a small (minute) bulla in "Zone A," but inflated ones from "Zone B" through "Zone D."

Summary of Species and Types

Five species and a subspecies of *Pseudocyclopidius* from 20 middle and upper Oligocene and 30 lower Miocene localities are here recorded:

1. *P. orellaensis,* new species, from Converse County, Wyoming; referred remains from Converse County, Wyoming; and Sioux County, Nebraska. (Oreodont faunal "Zone A" of Brule Formation.)

HOLOTYPE: Skull, F:A.M. 45528. Figures 36, 39.

2. *P. frankforteri,* new species, from Shannon County, South Dakota; referred remains from Shannon, Jackson, and Washabaugh counties, South Dakota; and Sioux and Morrill counties, Nebraska. ("Zone D" of Brule.)

HOLOTYPE: Skull and mandible, F:A.M. 45500. Figures 36, 37, 39, 40.

3. *P. major* (Leidy), from near Eagle Nest Butte, "White River," South Dakota; referred remains from Shannon and Washabaugh counties, South Dakota; Sioux, Scotts Bluff, Banner, and Morrill counties, Nebraska; and Weld County, Colorado. (Lower Gering Formation or deposits equal in age.

HOLOTYPE: Left maxilla, A.N.S.P. 10941. Figures 36, 39.

4. *P. lullianus* (Thorpe), from Niobrara County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; and Banner, Scotts Bluff, and Morrill counties, Nebraska. (Upper Gering.)

HOLOTYPE: Skull and mandible, Y.P.M. 10117.

4a. *P. lullianus expiratus,* new subspecies, from Converse County, Wyoming; referred remains from Converse and Niobrara counties, Wyoming; and Sioux and Morrill counties, Nebraska. (Monroe Creek.)

HOLOTYPE: Partial skull and mandible, F:A.M. 45598. Figures 36, 37, 39, 40.

5. *P. quadratus* (Koerner), from Meagher County, Montana. (Approximately equal in age to upper part of Gering.)

HOLOTYPE: Anterior portion of skull, Y.P.M. 13960.

DETAILED LISTS OF TYPES, REFERRED SPECIMENS AND SYNONYMY

PSEUDOCYCLOPIDIUS

TOTAL AVAILABLE SPECIMENS: 248[1]

1. **Pseudocyclopidius orellaensis,**[2] new species

From oreodont faunal "Zone A" of the Brule Formation, Converse County, Wyoming; referred remains from Converse County, Wyoming; and Sioux County, Nebraska

Description

SKULL: Small in size; dolichocephalic; brain case laterally expanded; nasals slightlly retracted anteriorly; lacrimal fossa moderately deep; nasal-facial vacuity present; muzzle elongated, narrow; auditory bulla inflated, laterally compressed.

MANDIBLE: (Unknown).

DENTITION: (Known from immature examples only). Premolars not crowded; external styles of superior molars less prominent than in other examples of *Pseudocyclopidius.*

LIMBS: Lightest and shortest of the genus.

MEASUREMENTS: Table 14 (p. 324).

ILLUSTRATIONS: Figures 36, 37, 39, 40, 43.

Discussion

The holotype and referred specimen of *Pseudocyclopidius orellaensis* are adolescents, inasmuch as both dental series contain dP^2–dP^4. It is realized that designating an immature specimen as a holotype is not the best practice, but the occurrence of a leptauchenin in oreodont faunal "Zone A" of the Brule is important. Previous to this report the leptauchenins as a group were believed to be restricted to "Zone D" of the Brule through the Gering and Monroe Creek deposits. The F:A.M. specimens were collected by George Sternberg in an area southeast of Douglas from which he has collected typical "Zone A" oreodonts included in the Miniochoerinae and the Merychoidodontinae.

[1] Includes 167 F:A.M. and 42 U.N.S.M. specimens.
[2] Named after the Orella deposits from which the holotype was secured.

The permanent M^1 and M^2 of both specimens are longer (anteroposterioly) than the same molars in *P. frankforteri* from "Zone D" of the Brule, a fact suggesting that the skull was longer than that of *P. frankforteri*. However, the *Pseudocyclopidius* line is the largest known of the leptauchenins. There is no question that these immature specimens are leptauchenins, as the nasal-facial vacuity is in evidence.

It is possible that *P. orellaensis* represents a phylum unknown above "Zone A" at this time, or a line that lived during Chadron times and disappeared during the period of "Zone A." There is no doubt that the specimens represent a new species, but the generic assignment may be questioned.

Three specimens are here recorded:

HOLOTYPE

Skull with C/(rt.)–dP^2–M^2. (I)	F:A.M. 45528	From oreodont faunal "Zone A" of Brule Formation, "nodular layer above white layer,"[1] 9 mi. SE. of Douglas, North Platte River drainage, Converse County, Wyoming; collected by George Sternberg, 1945. Figures 36, 37, 39

REFERRED FROM (A) CONVERSE COUNTY, WYOMING; AND (B) SIOUX COUNTY, NEBRASKA

A. FROM TYPE AREA, NORTH PLATTE RIVER DRAINAGE, 8 MILES SOUTHEAST OF DOUGLAS, 15 FEET ABOVE NODULAR LAYER, CONVERSE COUNTY, WYOMING

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with C/–dP^2–M^2, mandible with P_1(br.)–dP_2–M_2, partial humerus, partial radius, partial ulna, partial tibia, astragalus, calcaneum, and partial pes. Figures 37, 40, 43 . . . . (I) F:A.M. 45637

B. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, U.N.S.M. COLL. LOC. SX-1, SIOUX COUNTY, NEBRASKA

MANDIBULAR RAMUS — U.N.S.M.

Partial left ramus with M_1(br.)–M_3. Figures 37, 40 . . . . (M+) 28230

2. **Pseudocyclopidius frankforteri**,[2] new species

From oreodont faunal "Zone D" of Brule Formation, Shannon County, South Dakota; referred examples from Shannon, Jackson, and Washabaugh counties, South Dakota; and Sioux and Morrill counties, Nebraska

Description

Skull: Smaller than in examples of *P. major;* frontals with less anterior intrusion of nasal-facial vacuity; malar shallower than in examples of *P. major;* auditory bulla well inflated but smaller than in other examples of genus with exception of *P. orellaensis.*

Mandible: Smaller, slightly lighter, and with less concave notch on inferior border than in examples of *P. major.*

Dentition: Series smaller, lighter, less hypsodont, and superior molars with less prominent styles than in examples of *P. major.*

Limbs: (Not well represented in collections). Approaching size of examples of *P. major.*

Measurements: Table 14 (p. 324).

Illustrations: Figures 36, 37, 39, 40, 53.

[1] The "white layer" of this area is considered to be the equivalent of the "Upper Purplish White Layer" in the Cheyenne and White River drainage areas to the east in Wyoming, and also in Nebraska and South Dakota. This latter layer is considered to be the Chadron-Brule contact.

[2] Named in honor of Mr. W. D. Frankforter, Associate Director of the Grand Rapids Public Museum, Grand Rapids, Michigan. Mr. Frankforter, who is a Research Associate in the University of Nebraska State Museum, is a former Assistant Curator of Vertebrate Paleontology and field leader in the Museum, and Instructor in the Department of Geology, University of Nebraska.

Discussion

Pseudocyclopidius frankforteri from oreodont faunal "Zone D" of the Brule is readily distinguished from the larger skull, larger and longer tooth series, and longer (anteroposteriorly) frontal of *P. major. Pseudocyclopidius frankforteri* is also noticeably different from *Hadroleptauchenia primitiva* from the same zone in that the latter has a smaller skull, shorter (anteroposteriorly) frontals, and decidedly lighter teeth.

It is of interest that examples of *P. frankforteri* from "Zone D" of the Brule are close in size to those of *H. shanafeltae* from the lower Gering, but other characters differ, thus placing the two forms in different phylogenetic lines.

Pseudocyclopidius frankforteri represents the largest leptauchenin from "Zone D" of the Brule. It is approximately equal in size to a medium-sized example of the Miniochoerinae from the same geologic zone.

The F:A.M. collection was made by Morris F. Skinner and associates, 1938–1940, 1945, 1950; and the U.N.S.M. specimens were collected by C. Bertrand Schultz and associates, 1934, 1938, 1950.

Twenty-nine specimens are here recorded:

HOLOTYPE

Skull with I^1–I^3 alv. and C/(rt.)–M^3 and mandible with I_1–I_3 rt. and /C(br.)–M_3. (w‡⁺)	F:A.M. 45500	From oreodont faunal "Zone D" of Brule Formation in "basal part of *Leptauchenia* beds below 1st white layer," on high divide near head of E. Fork of Corral Draw, ¾–1¼ mi. S. of Cottonwood Pass, White River drainage, Shannon County, South Dakota; collected by Ralph Mefferd and Morris Skinner, 1940 Figures, 36, 37, 39, 40

REFERRED FROM (A) SHANNON, (B) JACKSON, AND (C) WASHABAUGH COUNTIES, SOUTH DAKOTA; (D) SIOUX AND (E) MORRILL COUNTIES, NEBRASKA

A. FROM WHITE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

From 1 Mi. S. of Cottonwood Pass:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Skull with I^1–M^3, mandible (attached) with I_1–M_3, partial humerus, partial radius, partial ulna, vertebrae, and ribs	(w+)	45518

SKULL AND MANDIBLE

Skull with P^1–M^3 and partial mandible with /C(rt.)–M_3	(w‡⁺)	45517

B. FROM CHEYENNE RIVER DRAINAGE, SHANNON COUNTY, SOUTH DAKOTA

From Range Running S. of Cottonwood Pass, Near E. Fork of Corral Draw:

SKULL

		F:A.M.
Skull with I^3–P^2 rt. and P^3–M^3	(w‡‡)	45501

From Between Heads of Cottonwood Creek and W. Fork of Big Corral Draw:

SKULL

Partial skull with C/–P^1 rt. and P^2–M^3	(w‡⁺)	56978

From Heads of Cottonwood Creek and Big Corral Draw:

SKULL AND MANDIBLE (ATTACHED)

Partial skull with P^3–M^3 and mandible (attached) with I_2–M_3	(w‡‡)	45513

From 7 Mi. E. of Rockyford, S. Side of White River:

2 SKULLS AND MANDIBLES (ATTACHED) — F:A.M.

Partial skull with P^1–M^3 and partial mandible with I_3–M_3 . . . . (w) 56979
Partial skull with I^3–C/ br. and P^1–M^3 and mandible with I_1–/C br. and P_1–M_3 . (w+) 45580

FROM 5 MI. NW. OF SHARP'S STORE:

SKULL AND MANDIBLE

Partial skull with P^1–M^3 (M^1 and M^2 br.) and fragments of mandible with M_1–M_2 . . . . (M+) 56980

FROM NE. OF INDIAN STRONGHOLD:

SKULL AND MANDIBLE (ATTACHED), IMMATURE

Partial skull with I^2–dP^2–M^3(germ) and mandible with P_1–dP_2–M_2 . . . . (I) 45516

C. FROM WHITE RIVER DRAINAGE, CEDAR PASS AREA, BASE OF *LEPTAUCHENIA* BEDS, JACKSON COUNTY, SOUTH DAKOTA

FROM W. OF CEDAR PASS:

SKULL AND MANDIBLE (ATTACHED) — F:A.M.

Partial skull with P^2–M^3 and mandible with P_1–M_3 . . . . (w) 45558

FROM $\frac{1}{4}$–1 MI. E. OF CEDAR PASS:

Partial skull with P^3–M^3 Figure 53 . . . . (–M) 45554

FROM NEAR CEDAR PASS:

2 SKULLS AND MANDIBLES

Partial skull with C/(rt.)–M^3 and mandible (attached) with P_3–M_3 . . . . (w) 56981
Cranium and partial mandible with P_3(rt.)–M_3 . . . . (w+) 56982

2 MANDIBULAR RAMI

Partial right ramus with P_4(br.)–M_3 . . . . (w‡) 56983
Partial right ramus with M_1–M_3(br.) . . . . (w‡) 56984

FROM $1\frac{1}{2}$ MI. NE. OF CEDAR PASS:

SKULL AND MANDIBLE, IMMATURE

Skull with C/–dP^2–M^3(erupt.) . . . . (I) 45556

D. FROM WHITE RIVER DRAINAGE, WASHABAUGH COUNTY, SOUTH DAKOTA

FROM HAY CREEK:

SKULL AND MANDIBLE — F:A.M.

Partial skull with P^1–P^2 rt. and P^3–M^3 and mandible with I_1–P_2 br. and P_3–M_3 . . (w) 45576

SKULL

Partial skull with C/–M^3. . . . . (w+) 45573

E. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–21:

MANDIBULAR RAMUS — U.N.S.M.

Partial right ramus with M_2–M_3 . . . . (w) 28269

FROM U.N.S.M. COLL. LOC. SX–22:

SKULL AND MANDIBLE		U.N.S.M.
Skull with P^1(br.)–M^3(erupt.) and mandible with /C(rt.)–M_3	(–M)	28401
SKULL		
Partial skull with C/–P^1 rt. and dP^2–M^2 (erupt.)	(I)	28587

F. FROM NORTH PLATTE RIVER VALLEY, PUMPKIN CREEK VALLEY, 12 MILES SOUTH OF BRIDGEPORT, MORRILL COUNTY, NEBRASKA

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with M_1–M_3	(W‡)	28229

3. **Pseudocyclopidius major** (Leidy)

From deposits equivalent to lower part of Gering Formation, near Eagle Nest Butte, Washabaugh County, South Dakota; referred remains from Shannon and Washabaugh counties, South Dakota; from lower Gering Formation, Sioux, Scotts Bluff, Banner, and Morrill counties, Nebraska; and Weld County, Colorado

Leptauchenia major Leidy, 1856b, p. 163; 1869, p. 124, pl. 12, figs. 1–6 (fig. 6 is *decora*, according to Leidy). Scott, 1890b, pl. 15, figs. 15–16. Thorpe, 1937, p. 238, pl. 35, fig. 1 (listed as *L. decora*), pl. 36, figs. 5–6, pl. 37, figs. 6–8.

Characters

Skull: Medium-sized; intermediate in size between examples of *P. frankforteri* and those of *P. lullianus*; frontals with greater anterior retraction than in examples of *P. frankforteri*; lacrimal fossa large and deep, approximately equal to that in *P. lullianus*, smaller and shallower than that in *P. frankforteri*; depression or pit above premolars more prominent than in last-mentioned species; malar deep below orbits, deeper than in *P. frankforteri*; auditory bulla more inflated than in *P. frankforteri*.

Mandible: Ramus slightly heavier, larger, and deeper than in examples of *P. frankforteri*; ramus lighter, smaller, and shallower than in *P. lullianus*.

Dentition: Series longer (anteroposteriorly), slightly more hypsodont, and more massive than in *P. frankforteri*, closer in these respects to those of *P. lullianus*; external styles of superior molars more pronounced than in *P. frankforteri*.

Limbs: Moderately long and heavy; shorter and lighter than examples of *P. lullianus*.

Measurements: Tables 14 and 15 (pp. 324 and 326).

Illustrations: Figures 36, 37, 39–41, 43.

Discussion

The original description of *Pseudocyclopidius major* by Leidy[1] was based on a series of specimens, including "the mutilated jaws of a larger species of *Leptauchenia*," which he had previously characterized under *L. decora*. Leidy mentioned, "In the upper jaw there are seven molars, forming nearly a continuous row, preceded by a small curved, conical canine." The specimen, A.N.S.P. 10941, compares favorably with Leidy's original description and measurements, and also with his later[2] description and illustrations. The present writers, therefore, have selected A.N.S.P. 10941 as the lectotype of *P. major*.

Leidy further stated: "In a specimen of the lower jaw belonging to *L. major*, and containing several true molars, there are also three premolars. The last of the latter [P_4] has been but a short time protruded. [The specimen in question is A.N.S.P. 10874; the roots of P_1–P_3 are present but evidently the teeth have been broken since Leidy's description.] . . . The intermediate pre-molar [P_3] belonged to the temporary series [the roots of P_1–P_3 which are now present suggest that all were permanent teeth] . . . the lower jaw indicated proves that the fragment of a lower jaw [A.N.S.P. 10891] containing several premolars, the canine, the incisive alveoli, previously referred to *L. decora*, does not belong to that genus." The present writers, however, have referred this particular specimen to *L. decora* (p. 280).

In a later discussion of the species, *P. major*, Leidy[3] stated: "*Leptauchenia* is an extinct genus . . . founded on some fossil remains discovered by Dr. Hayden in 1855, on one of the

[1] 1856b, p. 163.
[2] 1869, pl. 12, figs. 4–5.
[3] 1869, p. 122.

tributaries of the White River, near Eagle Nest Butte, in a formation attributed by him to Bed D of the Miocene . . . The fossils are more fractured and crushed, and more friable than those of *Oreodons* and their associates from the Mauvaises Terres [White River]. The matrix is also somewhat different from that of most of the latter, and resembles that attached to the remains of *Oreodon major* [= *Ustatochoerus major*]." The quoted passage indicates that Leidy considered the matrix to be more like the Miocene-Pliocene sediments than the clays of the Oligocene.

Most authors, including Loomis,[1] Schlaikjer,[2] and Thorpe,[3] considered *P. major* as occurring in the upper Brule, Hay,[4] however, recorded the species from the "Oligocene (Upper) or Miocene (Lower)." With the additional material now available from both the Brule and Gering formations, the lectotype, A.N.S.P. 10941, as well as all of Leidy's cotypes, compares favorably with other specimens from the lower part of the Gering Formation.

Additional material of *Pseudocyclopidius major,* in the collections of the Academy of Natural Sciences of Philadelphia, was figured by Leidy in 1869. The partial skull, A.N.S.P. 10942, was illustrated as figure 1 on plate 12, and the mandible, A.N.S.P. 10871, as figures 2–3 on the same plate. Additional preparation of the mandible has shown that the skull and mandible, A.N.S.P. 10942 and 10871, belonged to the same individual. The skull and ramus, A.N.S.P. 10940, also were illustrated by Leidy on plate 12 as figure 6. The present writers obtained permission from Horace Richards, Curator of Paleontology in the Academy of Natural Sciences of Philadelphia, to separate the skull and ramus, which were still partially embedded in the original matrix. Leidy[5] had considered the specimen as an adult example of *Leptauchenia decora,* and Thorpe[6] listed and illustrated it is one of the cotypes of the same species. The preparation of the specimen has made it possible to see the crowns of the teeth for the first time. The dentition is immature (P^1–dP^2–M^2 with dP^2 and dP^3 broken, and M_2 broken), and it is now evident that the specimen is an adolescent example referable to *P. major.*

The examples of *P. major* have skulls that are definitely longer than those of *H. shanafeltae* from the lower Gering, and slightly larger than those of *H. densa* from the upper Gering. It should be noted that *P. frankforteri* from oreodont faunal "Zone D" of Brule was approximately equal in size to *H. shanafeltae* from the lower Gering, but the skulls of *P. major* are larger than those of *H. densa* from the next higher geologic zone, indicating that the *Pseudocyclopidius* phylum evolved at a more rapid rate than *Hadroleptauchenia.*

The UN.S.M. collection (1932–1937) was made by E. L. Blue, Frank W. Crabill, Frank R. Denton, Loren C. Eiseley, Gordon Graham, Robert Kubicek, Robert Long, John Mercer, Marian and Bertrand Schultz, Mylan Stout, S. R. Sweet, Lloyd G. Tanner, Harry Tourtelot, Eugene Vanderpool, Lynn Robert Wolfe, and associates. The U.N.S.M. specimens (1950, 1951, 1955, 1957) were collected by John DeHaes, William Derieg, Jerry Folsom, W. D. Frankforter, Cyril Harvey, Edward F. Sabatka, C. Bertrand Schultz, Lloyd G. Tanner, Loren Toohey, and associates. The F:A.M. examples from South Dakota were recovered by Morris F. Skinner and associates, 1955; and those from Colorado, by Charles H. Falkenbach and associates, 1955.

Forty-six specimens are here recorded:

LECTOTYPE

Left maxilla with C/–M^3. (w+)	A.N.S.P. 10941	From deposits considered to be equivalent to lower part of Gering Formation, near Eagle Nest Butte, White River drainage, Washabaugh County, South Dakota; collected by F. V. Hayden, 1855 Figured by Leidy, 1869, pl. 12, figs. 4–5; Thorpe, 1937, pl. 36, figs. 5–6 This report, figures 36, 39

[1] 1925a, p. 247.
[2] 1935, pp. 167–168.
[3] 1937, p. 238.
[4] 1930, p. 789.
[5] 1869, fig. 6, pl. 12.
[6] 1937, p. 235.

REFERRED FROM (A) GENERAL TYPE AREA, (B) WASHABAUGH, (C) JACKSON, AND (D) SHANNON COUNTIES, SOUTH DAKOTA; (E) SIOUX, (F) SCOTTS BLUFF, (G) BANNER, AND (H) MORRILL COUNTIES, NEBRASKA; AND (I) WELD COUNTY, COLORADO

A. FROM GENERAL TYPE AREA, WHITE RIVER DRAINAGE, ?WASHABAUGH COUNTY, SOUTH DAKOTA

(5 COTYPES OF LEIDY)

SKULL AND MANDIBLE		A.N.S.P.
Partial skull with I^2–P^2 rt. and P^3–M^3 (all br.)	(w+)	10942
Mandible with I_1–I_3 rt. and /C–M_3	(w+)	10871

The above two specimens are from one individual. Figured by Leidy, 1869, pl. 12, figs. 1–3; Thorpe, 1937 pl. 37, figs. 6–8.

3 MANDIBULAR RAMI		
Partial mandible with P_1–P_3 rt. and P_4–M_2	(−M)	10874
Partial left ramus with M_1(br.)–M_3	(w)	10872
Partial right ramus with M_1(br.)–M_3(br.)	(w)	10873

SKULL AND MANDIBLE, IMMATURE		
Partial skull with P^1–dP^2–M^2 (dP^2 and dP^3 br.) and partial left ramus with M_2(br.) Figure 39	(I)	10940

The above specimen was referred to *Leptauchenia decora* by Leidy, 1869, pl. 12, fig. 6; Thorpe, 1937, pl. 35, fig. 1 (Thorpe considered this specimen to be the "genocotype" of *L. decora*).

B. FROM WHITE RIVER DRAINAGE, 30 FEET ABOVE FIRST WHITE LAYER, NORTHWEST OF QUIVER HILL, WASHABAUGH COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE (ATTACHED)		F:A.M.
Partial skull with I^3 and P^2–M^3 and mandible with P_1–M_3	(w)	56986

C. FROM WHITE RIVER DRAINAGE, ¼ TO 1 MILE EAST OF CEDAR PASS, JACKSON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE		F:A.M.
Partial skull with P^4–M^3 (M^1–M^2 br.) and mandible with P_2(br.)–M_3	(w+)	45537

2 SKULLS AND MANDIBULAR RAMI (ATTACHED)		
Anterior portion of skull with C/(br.)–M^3 (P^1 alv.) and partial mandible with P_1–M_3	(w‡)	45532
Partial skull with C/(br.)- M^3 and mandible with I_1–I_3 rt. and /C–M^3	(w)	45534

2 SKULLS		
Partial skull with P^3–M^3	(w‡)	45533
Partial skull with C/(rt.)–M^3 (P^1 and M^1 br.)	(w+)	45535

D. FROM WHITE RIVER DRAINAGE, 70 FEET ABOVE BASE OF FIRST WHITE LAYER, SOUTH END OF SHEEP MOUNTAIN, SHANNON COUNTY, SOUTH DAKOTA

SKULL AND MANDIBLE		F:A.M.
Inferior, anterior portion of skull with P^1–M^3 and partial mandible with P_3–M_3	(w)	56985

E. FROM WHITE RIVER DRAINAGE, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–22:

MAXILLA		U.N.S.M.
Left maxilla with C/(rt.)–M^3	(M)	28588

E′. FROM CHEYENNE RIVER DRAINAGE, HAT CREEK BASIN, SIOUX COUNTY, NEBRASKA

FROM U.N.S.M. COLL. LOC. SX–4:

MANDIBLE		U.N.S.M.
Partial mandible with P_1–P_2 rt. and P_3–M_3	(w)	28589

F. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM SW. OF SCOTTS BLUFF MONUMENT:

MAXILLAE AND MANDIBLE		U.N.S.M.
Partial right and left maxillae with P^1–M^3 and partial mandible with P_3(br.)–M_3	(w)	28590

G. FROM NORTH PLATTE RIVER DRAINAGE, NORTH SLOPE OF WILDCAT RIDGE, BANNER COUNTY, NEBRASKA

FROM 1 MI. W. OF U.N.S.M. COLL. LOC. MO–110:

SKULL		U.N.S.M.
Partial skull with P^2–M^3	(M+)	28402

FROM U.N.S.M. COLL. LOC. BN–102:

SKULL		
Inferior, anterior portion of skull with P^2(br.)–M^3	(w‡)	28591
3 MANDIBULAR RAMI		
Partial right ramus with M_1–M_2	(w)	28250
Partial left ramus with M_1–M_3(br.)	(w+)	28592
Partial left ramus with P_1–P_2 alv. and dP_3–M_2	(I)	28260

G′. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, BANNER COUNTY, NEBRASKA

FROM 2 MI. E. OF HUBBARD GAP:

MANDIBULAR RAMUS		U.N.S.M.
Partial left ramus with P_1–P_3 alv. and P_4(erupt.)–M_2	(I)	28227

H. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, WILDCAT RIDGE AREA, MORRILL COUNTY, NEBRASKA

FROM U.N.S.M COLL. LOC. MO–103:

MAXILLA		U.N.S.M.
Partial left maxilla with P^2–M^1	(w)	28412
MANDIBULAR RAMUS		
Partial left ramus with I_3–P_2 alv. and dP_3–M_2	(I)	28593

FROM U.N.S.M. COLL. LOC. MO–104 (F:A.M. COLL. LOC. "EAST SIDE OF ROUNDHOUSE ROCK"), "15′ ABOVE BASE OF GERING":

SKULL AND MANDIBLE, IMMATURE		
Inferior, anterior portion of skull with C/-dP^1-M^2 (germ) and partial mandible with I_1-dP_2-M_2 (erupt.)	(I)	F:A.M. 56987
2 SKULLS		
Partial skull with P^1-M^3	(w+)	56988
Anterior portion of skull with C/-dP^2-M^3 (germ) (P_4 erupt.)	(I)	U.N.S.M. 28594

MANDIBLE		U.N.S.M.
Partial mandible with P_1 (rt.)-M_3 (P_2 rt., P_3 alv.)	(w‡)	28595

FROM U.N.S.M. COLL. LOC. MO–105:

MAXILLA

Partial left maxilla with M^1-M^2 . . . . (−M) 28596

FROM U.N.S.M. COLL. LOC. MO-106:

SKULL, MANDIBLE, AND SKELETON

Skull with C/(rt.)–M^3 and mandible with I_2–M_3 (P_1 br.) and most of skeleton. Figures 36, 37, 40, 43 . . . . (w+) 1081

This skeleton is mounted and is on display in the University of Nebraska State Museum.

MANDIBLE

Partial mandible with P_4–M_3 . . . . (w+) 28597

FROM U.N.S.M. COLL. LOC. MO–107:

MANDIBULAR RAMUS

Partial left ramus with M_2–M_3 . . . . (w) 28598

FROM U.N.S.M. COLL. LOC. MO–108:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Skull with I^2–M^3, mandible with P_2–M_3, humerus, radius, 2 femora, 2 tibiae (1 partial), 2 astragali, 2 calcanea, and vertebrae. Figures 36, 37, 39–41, 43 . . . . . (w‡) 1080

The above skull exhibits no evidence of three superior incisors.

SKULL

Partial skull with P^1–M^3 . . . . (w+) 28599

MAXILLA

Partial right maxilla with dP^3(rt.)–M^2(erupt.) . . . . (I) 28600

MANDIBULAR RAMI

Partial mandible with P_1–M_3 (P_2–P_4 erupt.) . . . . (−M) 28216

Partial left ramus with P_1–P_4 alv. and M_1–M_3 . . . . (w) 28601

FROM 1 MI. W. OF U.N.S.M. COLL. LOC. MO–108:

MAXILLA

Partial left maxilla with P^3–M^3 (P^4–M^1 alv.) . . . . (w‡) 28239

FROM SW. OF BRIDGEPORT, WILD CAT RANGE AREA (IN VICINITY OF MO–103):

PARTIAL SKULL

Anterior portion of skull with C/–M^3 . . . . (w‡) 28608

2 MAXILLAE

Partial right maxilla with P^2–M^1 rt. and M^2–M^3. . . . . (w+) 28602

Partial right maxilla with P^4–M^1 rt. and M^2–M^3. . . . . (w+) 28603

MANDIBULAR RAMUS

Partial right ramus with P_1–P_2 rt. and P_3–M_3 . . . . (w+) 28206

H′. FROM PLATTE RIVER DRAINAGE, 2 MILES EAST AND 1½ MILES NORTH OF BROADWATER, MORRILL COUNTY, NEBRASKA

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with P_3–M_3	(M)	28245

I. TENTATIVELY REFERRED FROM SOUTH PLATTE RIVER DRAINAGE, EAST OF ROCKPORT, HIGH CHANNEL DEPOSITS, WELD COUNTY, COLORADO

2 MAXILLAE		F:A.M.
Partial left maxilla with P^1–dP^2–M^1(br.)	(I)	57160
Partial left maxilla with dP^2–dP^3	(I)	57161
MANDIBULAR RAMUS		
Partial right ramus with P_1–P_4 alv. and M_1	(–M)	57162

4. **Pseudocyclopidius lullianus** (Thorpe)

From upper part of Gering Formation, Niobrara County, Wyoming; referred remains from Niobrara, Goshen, and Laramie counties, Wyoming; Banner, Scotts Bluff, and Morrill counties, Nebraska

Cyclopidius lullianus THORPE, 1921b, p. 413, figs. 1–3; 1925, p. 72, fig. 2; 1937, p. 247, figs. 172–177, pl. 49, fig. 1. LOOMIS, 1925a, p. 242, figs. 1–2.

CHARACTERS

SKULL: Larger than in examples of *P. major,* posterior portion elongated; sagittal crest higher than in examples of *P. major*; brain case more depressed than in other examples of genus; orbit small; malar deep below orbit, deeper than in other leptauchenins; malar with anterior downward projection more abrupt than in *P. major*; muzzle with tendency to be more shovel-like than in other examples of genus.

MANDIBLE: Largest, heaviest, and deepest of genus; ascending ramus exceedingly high.

DENTITION: Approximately equal to that of *P. major.*

LIMBS: Longest and heaviest of genus.

MEASUREMENTS: Tables 14 and 15 (pp. 324 and 326).

ILLUSTRATIONS: Figures 36, 37, 39, 40, 43.

DISCUSSION

Thorpe's[1] original description and his 1937 report[2] gave specific characters which are chiefly characteristic of the genus *Pseudocyclopidius.* Some of his characters are here considered as evidence of individual variation. As noted by Thorpe, the auditory bulla of *P. lullianus* is the most inflated of all the oreodonts. Thorpe also mentioned that the lower dentition contained only two incisors. The present writers have examined the ramus of the holotype and noted that the lower incisors were all absent. Material here referred to *P. lullianus* contains three lower incisors. No leptauchenins (or other oreodonts) have fewer than three lower incisors.

Thorpe[3] unintentionally referred the skeleton used in Loomis' illustrations[4] of *P. lullianus* to *Hadroleptauchenia densa,* but retained the specimen number "A.C. 22–595" (= new Amherst College Museum Number 7695), which is the number of the holotype of *H. densa.* The number of the skeleton of *P. lullianus* is A.C. 7679. Loomis' figure 2 illustrates a five-toed forefoot of *P. lullianus* (A.C. 7679). The specimen F:A.M. 57090 (fig. 43, present report) also contains five toes in the forefoot.

Loomis[5] concluded that the dentition of *P. lullianus,* ". . . is hypsodont, the most so of any oreodont." Thorpe,[6] considering the same species, stated, "The dentition is markedly hypsodont; in fact, relative to the size of the skull, the teeth are longer than those of any other oreodont." The present authors believe that *Sespia* (p. 239) has the most hypsodont dentition of all oreodonts. The teeth are more hypsodont than those of the recent horse (see fig. 42, present paper).

Loomis[7] discussed the Muddy Creek area and the geology which he compared, respectively, with the Goshen Hole of Wyoming and the Lower Rosebud of South Dakota. He reported: "The species [*Hadroleptauchenia densa*] is erected for some 20 specimens from both Muddy Creek,* or as it is often designated, the Spanish Mines, and from the south side of Goshen Hole, both localities in Wyoming, and

[1] 1921b, p. 413.
[2] 1937, p. 146.
[3] 1937, fig. 172, pl. 49, fig. 1.
[4] 1925a, figs. 1–2.
[5] 1925a, p. 242.
[6] 1937, p. 240.
[7] 1925a, p. 245.

both representing Lower Rosebud time, as indicated by the presence of *Mesoreodon megalodon, Merychyus curtus,* and *Eporeodon relictus,* all species characteristics of the Lower Rosebud further east in South Dakota." Loomis' footnote concerning "Muddy Creek*" stated, "This bed has been erroneously referred to by Lull, Thorpe, and myself as Lower Harrison in our earlier papers." The present writers consider the formation where both *H. densa* and *P. lullianus* remains are found (Spanish Diggings [= "Spanish Mines"] and Little Muddy Creek area, and also the chief fossil-bearing deposits from the south side of Goshen Hole) as upper Gering. Little Muddy Creek is a tributary of Muddy Creek, and the majority of the fossils found on the latter are from the Monroe Creek Formation. The Frick Laboratory has extensive collections made under the leadership of Charles H. Falkenbach (1930–1961) from all these Wyoming localities. Both of the present writers have spent considerable time together in these collecting localities dating the deposits and making geologic sections for comparison with similar deposits in adjacent areas in Nebraska, South Dakota, and Wyoming. The term "Rosebud," as used by Loomis and others, includes deposits equal to the Gering, Monroe Creek, Harrison, and even Marsland deposits.[1]

It should be pointed out that, in the present report as well as in the others concerned with the revision of the oreodonts, the "Muddy Creek" locality in Wyoming follows Muddy Creek proper in a northeast-southwest direction. The southwest portion of the deposits along Muddy Creek are mostly Monroe Creek Formation, with a small amount of upper Gering at the base. The farther northeast one goes along Muddy Creek, the thicker the Gering deposits become and the thinner the Monroe Creek. Along Little Muddy Creek, a tributary of Muddy Creek, the deposits are all Gering. The Spanish Diggings, or "Mines," are on the northeast portion of this drainage, and high up along the Hartville Uplift there is a small area of Monroe Creek deposits approximately 25 feet in thickness.

The three species mentioned by Loomis have been included in the oreodont revision and have been referred as follows: *Mesoreodon megalodon* Peterson from the Monroe Creek (Schultz and Falkenbach 1949, p. 145); *"Merychyus" curtus* Loomis = *?Oreodontoides curtus* (Loomis) from the Harrison or deposits equal in age (*idem,* 1947, p. 253); and *"Eporeodon" relictus* Loomis = *Paramerychyus relictus* (Loomis) from Harrison age deposits (*idem,* 1947, p. 249).

The F:A.M. specimens were collected by John C. Blick, Everett De Groot, Charles H. Falkenbach, John Lynch, Gene Roll, George Sternberg, Nelson J. Vaughan, and associates, 1938, 1943, 1945, 1948, 1954; and the U.N.S.M. examples, by C. Bertrand Schultz and associates, 1933–1937.

One hundred and forty-four specimens are here recorded:

HOLOTYPE

Partial skull with I^2–M^3 and mandible with $C/$–M_3. (w)	Y.P.M. 10117	From upper part of Gering Formation, Muddy Creek, "Spanish Mines," Niobrara County, North Platte River drainage, Wyoming; collected by R. S. Lull, 1908 Figured by Thorpe, 1921b, figs. 1–3; 1925, fig. 2; 1937, figs. 172–177, pl. 49, fig. 1

REFERRED FROM (A) NIOBRARA, (B) GOSHEN, AND (C) LARAMIE COUNTIES, WYOMING; (D) BANNER, (E) SCOTTS BLUFF, AND (F) MORRILL COUNTIES, NEBRASKA

A. FROM NORTH PLATTE RIVER DRAINAGE, NIOBRARA COUNTY, WYOMING

FROM LITTLE MUDDY CREEK:

2 ASSOCIATED INDIVIDUALS		F:A.M.
Partial skull with P^4(br.)–M^3 and partial mandible (attached) with P_4(br.)–M_3 . .	(w)	56989A
Fragmentary skull with P^3(br.)–M^3 and partial left ramus with P_4–M_1 br. and M_2–M_3	(w‡)	56989B

[1] Schultz and Falkenbach, 1949, chart 3, p. 83.

4 ASSOCIATED INDIVIDUALS

		F:A.M.
Partial skull with C/–M^3 (P^1, M^2–M^3 br.) and partial mandible with I$_1$–M$_3$.	(w+)	56990A
Skull with C/–M^3	(M+)	56990B
Partial skull with P^3(br.)–M^3	(M)	56990C
Partial mandible with P$_1$ and dP$_4$–M$_2$	(I)	56990D

2 SKULLS, MANDIBULAR RAMI, AND SKELETAL ELEMENTS

Partial skull with C/–dP^1–M^2 and partial right ramus with dP$_2$–M$_2$, partial humerus, partial radius, 2 partial ulnae, and partial manus	(I)	56991
Partial skull with I^3–P^1 rt. and P^2–M^3, mandible with /C(rt.)–M$_3$, partial humerus, partial radius, partial ulna, partial manus, partial femur, and partial pelvis	(−M)	56992

25 SKULLS AND MANDIBLES

Partial skull with C/–M^3 (P^1 alv.) and mandible with I$_1$–M$_3$. Figures 37, 40	(w‡)	34484
Skull with C/–M^3 and mandible with I$_1$–M$_3$ (P$_1$ rt.)	(w‡‡)	45600
Partial skull with I^2–M^3 and mandible with I$_1$–M$_3$.	(w‡)	56993
There is no evidence that I^1 was ever present in the above skull.		
Skull with C/(erupt.)–dP^1–M^3 (germ) and fragments of mandible with M$_1$–M$_3$ (erupt.)	(I)	56994
Skull with I^3(rt.)–M^3 and partial mandible (attached) with P$_2$–M$_3$.	(w)	56995
Fragmentary skull with P^3–M^3 and mandible (attached) with /C–M$_3$ (P$_2$ alv.)	(M+)	56996
Partial skull with P^1–dP^2–M^2 and mandible (attached) with dP$_2$–M$_2$	(I)	56997
Partial skull with C/(br.), P^1–P^4 erupt. and M^1–M^2 and mandible (attached) with P$_1$–dP$_3$–M$_2$ (P$_3$–P$_4$ erupt.)	(I)	56998
Inferior portion of skull with C/–M^3 and mandible (attached) with I$_1$–M$_3$	(w)	56999
Fragmentary skull with I^3–M^3 and mandible with /C–M$_3$	(w+)	57000
Anterior portion of skull with C/–P^1 br. and P^2–M^3 and partial mandible (attached) with P$_3$–M$_3$	(w)	57001
Inferior portion of skull with C/–M^3 and partial mandible with P$_1$–M$_3$	(M+)	57002
Left side of skull with P^4–M^3 (M^1 br.) and mandible (attached) with P$_4$–M$_3$	(w+)	57003
Partial skull with P^4–M^3 and mandible (attached) with P$_1$–P$_3$ rt. and P$_4$–M$_3$	(w)	57004
Skull with C/–M^3(germ) (P^2–P^4 erupt.) and partial mandible with P$_1$–dP$_4$–M$_2$ (P$_2$–P$_3$ alv.)	(I)	57005
Partial skull with P^1–M^3 and mandible (attached) with P$_1$(br.)–M$_3$	(M)	57006
Inferior, anterior portion of skull with C/–M^3 and partial mandible (attached) with /C–M$_3$	(M+)	57007
Inferior, anterior portion of skull with C/–dP^2–M^3(germ) and mandible with /C–P$_2$ br. and dP$_3$–M$_3$(germ)	(I)	57008
Anterior portion of skull with C/–M^3 and mandible with I$_1$–/C rt. and P$_1$–M$_3$	(w‡)	57009
Fragmentary skull with M^1(br.)–M^3 and mandible (attached) with P$_4$–M$_3$	(−M)	57010
Inferior, anterior portion of skull with P^1–M^3 and mandible with I$_1$–P$_1$ rt. and P$_2$ (alv.)–M$_3$	(w+)	57011
Partial skull with C/(rt.)–M^3 and right ramus with P$_1$–M$_3$	(w+)	57012
Partial skull with P^4–M^3 and mandible with I$_2$–P$_2$ br. and P$_3$–M$_3$	(w+)	57153
Skull with I^2–I^3 rt. and C/–M^3 (P^1 rt.), and mandible with I$_2$–M$_3$	(w+)	57013
Skull with I^2–I^3 br. and C/(erupt.)–dP^4–M^1, and mandible with I$_1$–I$_3$ rt. and /C (erupt.)–dP$_4$–M$_1$	(I)	57020

21 SKULLS

9 partial skulls with

C/–M^3.	(w‡)	34486
I^2(rt.)–M^3. Figures 36, 37, 39	(w‡$^+$)	45597
C/–P^1 rt. and P^2–M^3	(w)	45599
I^3–M^3	(w+)	57014
C/–M^3.	(w+)	57015
C/–M^3.	(−M)	57016
P^4(erupt.)–M^2	(I)	57017
C/(rt.)–M^3	(w+)	57018

		F:A.M.
C/–M^3(erupt.)	(−M)	57019
There is no evidence that I^1 was ever present in the above skull.		
P^4–M^1 rt. and M^2–M^3	(M+)	57021
9 anterior portions of skull with		
P^1–M^3	(M+)	57022
C/(rt.)–M^3	(M+)	57023
C/–dP^1–M^2	(I)	57024
C/–P^1 br. and P^2–M^3	(W)	57025
C/–M^3(erupt.)	(−M)	57026
P^3(rt.)–M^2	(M+)	57027
C/–M^3	(W)	57028
C/(br.)–dP^2–M^2	(I)	57029
P^1(rt.)–M^3(erupt.)	(−M)	57154

23 MAXILLAE

9 partial right maxillae with		
C/–M^3	(W)	57030
P^4–M^3	(W‡$^+$)	57031
dP^4–M^2	(I)	57032
dP^1–M^2	(I)	57033
dP^4–M^2 (P^4 germ)	(I)	57034
dP^4(br.)–M^1	(I)	57035
dP^4–M^1	(I)	57036
dP^2–M^2(germ)	(I)	57037
P^2–M^2	(W+)	57038
14 partial left maxillae with		
P^4–M^3 (M^1 alv.)	(W+)	57039
M^1–M^3	(W+)	57040
M^3	(W‡)	57041
M^2–M^3 br.	(W‡)	57042
M^1–M^3 br.	(M)	57043
P^4–M^3(erupt.)	(−M)	57044
dP^4–M^1 (P^4 erupt.)	(I)	57045
M^1–M^2	(M)	57046
M^1–M^2	(M)	57047
P^2(rt.)–M^3	(W‡)	57048
dP^3–M^2	(I)	57049
dP^2–dP^4	(I)	57050
C/(erupt.)–P^1–dP^2–dP^4	(I)	57051
P^1–dP^2–M^1	(I)	57052

7 MANDIBLES

7 partial mandibles with		
P_3–M_3	(M)	57054
I_1–M_3(erupt.) (P_2–P_4 erupt.)	(−M)	57055
P_1–M_3	(M)	57056
I_1–P_2 rt. and P_3–M_3	(W‡$^+$)	57057
/C–M_3	(W‡$^+$)	57058
P_2(alv.)–M_3(br.)	(W‡)	57059
dP_3–M_2	(I)	57060

21 MANDIBULAR RAMI

11 partial right rami with		
P_4–M_2(br.)	(W)	57062
M_2–M_3	(W+)	57063
/C–P_1 rt. and P_3–M_2	(W‡)	57064
P_4–M_3	(W‡)	57065

		F:A.M.
P_3(br.)–M_2	(w+)	57066
I_1–P_2 alv. and P_3–M_2	(w‡)	57067
M_1(br.)–M_3	(M)	57068
dP_3–M_2	(I)	57069
P_1(erupt.)–dP_2–M_1	(I)	57070
dP_4–M_3(germ)	(I)	57071
dP_3–M_1	(I)	57072
10 partial left rami with		
I_3–P_2 rt. and P_3–M_2(rt.) (M_1 rt.)	(M)	57073
M_1–M_3	(w‡)	57074
M_1–M_2	(w)	57075
P_1–M_3	(w‡)	57076
P_2–M_2	(w‡+)	57077
I_1–/C alv. and P_1–dP_4–M_3(erupt.)	(I)	57078
I_3–/C alv. and P_1–dP_2–M_2	(I)	57079
M_1–M_2	(w)	57080
M_1–M_2	(–M)	45604
dP_4–M_2	(I)	57081

From Muddy Creek (Gering Formation):

SKULL AND MANDIBLE

Skull with I^3–M^3 and mandible with /C–P_1 br. and P_2–M_3	(M)	57082

From Willow Creek:

4 SKULLS AND MANDIBULAR RAMI

Partial skull with P^1(br.)–M^3 and mandible with P_2(br.)–M_3 (P_3–P_4 br.)	(w+)	57083
Partial skull with P^2–M^3 and mandible (attached) with P_2–M_3 (P_3–M_2 br.)	(w)	57084
Fragmentary skull with P^3(br.)–M^3 and partial right ramus with P_1–P_2 br. and P_3–M_3 (br.)	(w‡+)	57085
Anterior portion of skull with C/–dP^2–M^2 and partial left ramus with P_1(br.)–dP_2–M_1	(I)	57086

2 SKULLS

Partial skull with P^3–M^3	(w)	57087
Skull with C/–dP^2–M^2	(I)	57088

MANDIBLE

Partial mandible with I_2 and /C–M_3 (P_1–P_2 br.)	(w)	34413

B. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, GOSHEN COUNTY, WYOMING

From 66 Mt., near Hagie, 35 Mi. S. and E. of Torrington (Collected by F. B. Loomis, A. C. Expedition, 1922):

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		A.C.
Skull with C/–M^3, mandible with P_1–M_3, and skeleton. Figured by Loomis, 1925a, figs. 1, 2; Thorpe, 1937, fig. 172, pl. 49	(w‡)	7679

The above skeleton is mounted in the Amherst College Museum. Thorpe considered this specimen to be the holotype of "*Cyclopidius densus*" (=*Hadroleptauchenia densa*). See discussion in present paper (p. 336).

From S. Side of 66 Mt.:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Skull with P^3–M^3, mandible (attached) with I_1–I_3 rt. and /C–M_3 (/C–P_1 br.), partial scapula, humerus, partial femur, tibia, and fragments	(w+)	57089

C. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, LARAMIE COUNTY, WYOMING

FROM TREMAIN AREA:

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

		F:A.M.
Posterior portion of skull, mandible with I_3–P_4 rt. and M_1–M_3, and most of skeleton.[1] Figure 43	(W)	57090

3 SKULLS AND MANDIBLES

Partial skull with P^2–M^3 and mandible with P_1–M_3	(W)	57091
Posterior portion of skull with M^1–M^3 and partial mandible with /C–P_2 rt. and P_3–M_3	(W)	57092
Partial skull with dP^1 and dP^3–M^3(germ) and I_3–dP_2–M_3(erupt.)	(I)	57093

5 SKULLS

Skull with I^3–M^3	(W+)	57094
Anterior portion of skull with I^3–M^3	(W+)	57095
Inferior, anterior portion of skull with M^1(br.)–M^3(erupt.)	(I)	57096
Anterior portion of skull with dP^2–M^2	(I)	57097
Inferior, anterior portion of skull with I^3–M^3(erupt.)	(−M)	57155

3 MAXILLAE

Partial right maxilla with P^4–M^3	(M)	57098
Partial right maxilla with dP^2–M^1	(I)	57099
Partial left maxilla with P^4–M^3	(M)	57100

3 MANDIBLES

3 partial mandibles with		
P_4–M_3	(W)	57101
I_2–M_3	(W+)	57102
P_4(br.)–M_3	(W+)	57103

MANDIBULAR RAMUS

Partial left ramus with dP_2(br.)–dP_4	(I)	57104

FROM ALBIN ROAD AREA, S. OF HORSE CREEK:

SKULL AND MANDIBLE

Partial skull with I^2–M^3 and mandible with I_3–M_3	(M+)	57105

2 MANDIBLES

Mandible with /C–M_3 (P_1 alv.)	(W)	57106
Partial mandible with P_1–M_3	(W+)	57107

FROM E. OF U. S. HIGHWAY NO. 85, S. OF HORSE CREEK:

SKULL

Partial skull with C/–P^1–dP^2–M^3(germ)	(I)	57108

FROM STINKING WATER CREEK:

MAXILLA

Partial left maxilla with P^4–M^3	(W+)	57109

[1] The skeleton was found "25′ below white layer," east of Tremain, Wyoming, along the Wyoming-Nebraska boundary line, but on the Wyoming side of the line, according to Charles H. Falkenbach. The F:A.M. field records indicate "Nebraska."

D. FROM NORTH PLATTE RIVER DRAINAGE, HORSE CREEK BASIN, BANNER COUNTY, NEBRASKA

FROM 15 MI. W. AND 8 MI. S. OF HARRISBURG:

MANDIBULAR RAMUS		F:A.M.
Partial right ramus with P_4–M_3 (P_4 and M_1 br.)	(w‡⁺)	57110

D′. FROM NORTH PLATTE RIVER DRAINAGE, PUMPKIN CREEK VALLEY, BANNER COUNTY, NEBRASKA

FROM S. SIDE OF 66 MT.:

SKULL AND MANDIBLE		F:A.M.
Partial skull with dP^3(br.)–M^2 and mandible with I_2–P_1–dP_2–M_2	(I)	57111
In the above mandible there is no evidence of three incisors.		

MANDIBLE		U.N.S.M.
Partial mandible with I_1–dP_3–M_2	(I)	28226

FROM BULL CANYON, 13 MI. W. OF HARRISBURG:

MANDIBLE		
Partial mandible with P_3–M_3	(w‡)	28242
MANDIBULAR RAMUS		
Left ramus with P_1–P_2 rt. and P_3–M_3	(w‡)	28604

FROM 1 MI. E. OF WRIGHT GAP:

MANDIBULAR RAMUS		
Partial left ramus with M_1–M_3	(w‡⁺)	28234

E. FROM NORTH PLATTE RIVER DRAINAGE, SCOTTS BLUFF COUNTY, NEBRASKA

FROM WILDCAT RIDGE AREA, S. OF LYMAN:

PARTIAL SKULL		F:A.M.
Inferior, anterior portion of skull with I^3–dP^2–M^2	(I)	43378

E′. FROM NORTH PLATTE RIVER DRAINAGE, MORRILL COUNTY, NEBRASKA

FROM N. SLOPE OF WILDCAT RIDGE, U.N.S.M. COLL. LOC. MO–110:

MANDIBLE		U.N.S.M.
Partial mandible with I_1(alv.)–M_3 (I_2–I_3 rt.)	(w‡)	28605

4a. **Pseudocyclopidius lullianus expiratus,**[1] new geologic subspecies

From Monroe Creek Formation, Converse County, Wyoming; referred remains from Converse and Niobrara counties, Wyoming

DESCRIPTION

SKULL: Tendency to be longer but similar to that of *P. lullianus.*

MANDIBLE: Same comparison as skull.

DENTITION: Similar to and within size range of species.

LIMBS: (Unknown).

MEASUREMENTS: Table 14 (p. 324).

ILLUSTRATIONS: Figures 36, 37, 39, 40, 53.

DISCUSSION

Pseudocyclopidius lullianus expiratus remains represent the last survivors of the phylum. The skull and mandible do not differ in characters from those of the species, except as

[1] The name indicates the last geologic appearance of the phylum.

noted above. This fact also has been noted in other subfamilies such as in the Desmatochoerinae; in *Megoreodon*,[1] for example, no apparent general morphologic changes are indicated between examples from the Gering Formation and those from the Monroe Creek Formation.

The absence of changes of characters is of as great importance as are actual modifications, and geologic subspecific names have been applied to emphasize this fact. In any phylogenetic line studied from a stratigraphic basis, the change in size of forms from one deposit to the next in the geologic sequence is perhaps the most important single character.

When additional specimens of the subspecies are available, they may demonstrate that the average skull is longer basally than skulls of *P. lullianus*, owing to the expansion of the posterior portion of the skull. This is noted in the comparison of examples of *P. frankforteri* and *P. major*.

The F:A.M. specimens from Wyoming were collected by Charles H. Falkenbach and associates, 1932–1939; and the F:A.M. examples from Nebraska and South Dakota, by Morris F. Skinner and associates, 1942. The U.N.S.M. mandibular ramus was found by C. Bertrand Schultz and associates, 1937.

Twenty-eight specimens are here recorded:

HOLOTYPE

Partial skull with P^1–M^3 and mandible with /C (br.)–M_3. (w‡⁺)	F:A.M. 45598	From Monroe Creek Formation, 3 mi. S. of Douglas, North Platte River drainage, Converse County, Wyoming; collected by George Sternberg, John C. Blick, and Charles H. Falkenbach, 1941 Figures 36, 37, 39, 40

REFERRED FROM (A) CONVERSE AND (B) NIOBRARA COUNTIES, WYOMING; (C) SIOUX AND (D) MORRILL COUNTIES, NEBRASKA

A. FROM TYPE AREA, 3 MILES SOUTH OF DOUGLAS, CONVERSE COUNTY, WYOMING

SKULL AND MANDIBLE

Anterior portion of skull with C/–M^3 (P^1 absent) and mandible with I_1–I_3 rt. and /C–M_3. Figures 37, 39, 40, 53 (in part)	(w)	F:A.M. 45601

MAXILLA, IMMATURE

Partial left maxilla with C/(erupt.)–P^1–dP^2–M^1	(I)	57112

2 MANDIBULAR RAMI, IMMATURE

Partial right ramus with P_3–dP_4–M_1	(I)	57113
Partial right ramus with dP_2–M_2	(I)	57114

B. FROM MUDDY CREEK AREA, NIOBRARA COUNTY, WYOMING

2 ASSOCIATED INDIVIDUALS

Inferior, anterior portion of skull with P^1–dP^2–M^1 and partial right ramus with dP_3–M_1	(I)	F:A.M. 57115A
Inferior, anterior portion of skull with P^3–M^3	(−M)	57115B

SKULL, MANDIBLE, AND SKELETAL ELEMENTS

Partial skull with I^3(br.)–M^3, mandible with I_1–M_3, partial scapula, humerus, and partial tibia. Figure 43.	(M+)	57116

This specimen has an extra tooth between P^1 and C/.

[1] Schultz and Falkenbach, 1954, pp. 171, 174.

SKULL AND MANDIBLE		F:A.M.
Skull with C/(br.)–M^3(erupt.) (P^2–P^4 erupt.) and mandible with P_2–M_3(erupt.) (P_3–P_4 erupt.)	(–M)	57117

2 SKULLS		
Partial skull with C/–M^3.	(W+)	57118
Partial skull with I^2–P^1–dP^2–M^2(erupt.)	(I)	57119

MAXILLA AND MANDIBULAR RAMI		
Partial right maxilla with P^4–M^3 and right ramus with /C–M_3 (P_2 alv.)	(M)	57121

9 MANDIBULAR RAMI		
3 partial mandibles with		
I_1–/C rt. and P_1–M_3	(M+)	57123
P_2–M_3	(M+)	57124
I_2–P_1 rt. and P_2–M_3	(W‡)	57125
4 partial right rami with		
dP_2–M_1	(I)	57126
dP_2–dP_4	(I)	57127
dP_4–M_2(br.)	(I)	57128
M_1–M_2	(–M)	57129
Partial left ramus with M_3 br.	(W‡)	57130

C. FROM NORTH PLATTE RIVER DRAINAGE, 5 MILES NORTHEAST OF BRIDGEPORT, MORRILL COUNTY, NEBRASKA

MANDIBULAR RAMUS		U.N.S.M.
Partial right ramus with P_1–dP_3–M_2 (P_1 alv.)	(I)	28606

D. FROM UPPER MONROE CREEK FORMATION, NORTH PLATTE RIVER DRAINAGE, LEDINGHAM RANCH, SIOUX COUNTY, NEBRASKA

2 SKULLS AND MANDIBULAR RAMI		F:A.M.
Inferior portion of skull with P^3–M^3 and partial mandible with P_4–M_3	(W)	57131
Right anterior portion ot skull with P^1–dP^1–M^2 and partial left ramus with M_1	(I)	57132

SKULL		
Partial skull with M^2–M^3	(W+)	57133

MANDIBLE AND LIMBS, IMMATURE		
Partial mandible with I_1–dP_2–M_3(germ), partial humerus, and partial femur	(I)	57134

MANDIBLE		
Partial mandible with P_2–M_3	(M)	57135

E. FROM WHITE RIVER DRAINAGE, MOUTH OF PORCUPINE CREEK CANYON, SHANNON COUNTY, SOUTH DAKOTA

MANDIBULAR RAMUS		F:A.M.
Partial right ramus with M_1(br.)–M_2	(W)	57136

The above specimen is not complete enough for definite identification, but this species is suggested by its size and other characters. Morris F. Skinner, the collector of the above specimen, considered the geologic occurrence as "near top of pink clay with small nodules and below ?Harrison or Monroe Creek-like bluffs."

5. **Pseudocyclopidius quadratus** (Koerner)

From deposits approximately equal in age to the upper part of Gering Formation, Meagher County, Montana

Cyclopidius quadratus KOERNER, 1940, p. 857, pl. 7, fig. 1.

CHARACTERS

SKULL: (Known from anterior, inferior portion only). Suggests size of that of *P. lullianus*; muzzle narrow.

MANDIBLE: (Known from immature individual only). Approximate size of that of *P. lullianus*.

DENTITION: Series larger than in examples of *Cyclopidius simus* and *C. emydinus*, close to those of *P. lullianus*.

LIMBS: (Unknown).

MEASUREMENTS: Table 14 (p. 324).

DISCUSSION

The skull of the holotype lacks the posterior portion, hence the length is unknown. The skull represents a larger species than either *Cyclopidius simus* or *emydinus*. The available measurements indicate that *P. quadratus* is closer to the size of examples of *P. lullianus* from the Great Plains. Perhaps *P. quadratus* represents a form from the central Great Plains that migrated to Montana and subsequently evolved there.

Koerner[1] proposed the new species *Cyclopidius quadratus* and based it primarily on the nearly equidimensional crown of M^1. In the leptauchenins the shapes of the crowns of M^1's vary according to the stage of wear.

It should be noted that Koerner considered that the specimens were from the "Deep River Formation, late Miocene." Leptauchenins, however, have not been recorded from deposits later than lower Miocene in age (Monroe Creek Formation or its equivalent). There are deposits equal in age to the Sheep Creek Formation in the White Sulphur Springs area (see p. 403), but no leptauchenins have been recorded from deposits of this age.

Two specimens are here recorded:

HOLOTYPE

Inferior, anterior portion of skull with I^3–M^2. (w)	Y.P.M. 13960	From lower portion of "Deep River Formation" in deposits approximately equal in age to the Gering, sect. 3, T. 10 N., R. 5 E., White Sulphur Springs, Smith River drainage, Montana; collected by Harold E. Koerner Figured by Koerner, 1940, pl. 7, fig. 1

REFERRED FROM TYPE AREA, SMITH RIVER DRAINAGE, WHITE SULPHUR SPRINGS, MEAGHER COUNTY, MONTANA

MANDIBULAR RAMUS		Y.P.M.
Left ramus with P_1–dP_2–M_2	(I)	13973

[1] 1940, p. 857.

EXPLANATION OF TEXT FIGURES 31–43

FIG. 31. Lateral, dorsal, and ventral views of skulls, and mandibular rami: *Sespia ultima,* new species, holotype, F:A.M. 45606 (M^3 from opposite side), from Monroe Creek Formation, Niobrara County, Wyoming; *S. nitida* (Leidy), holotype, A.N.S.P. 10870, from ?deposits equal in age to upper part of Gering Formation, South Dakota, and referred, F:A.M. 45622, from upper part of Gering Formation, Laramie County, Wyoming; *S. marianae,* new species, holotype, U.N.S.M. 28420A, from lower part of Gering Formation, Morrill County, Nebraska; *S. californica* (Stock), holotype, U.C. 27720 (lateral view only, after Stock), from deposits approximately equal in age to Gering Formation, Ventura County, California; *S. heterodon* (Cope), holotype, A.M. 8131, from deposits approximately equal in age to Gering Formation, Montana; *Megasespia middleswarti,* new species, holotype, U.N.S.M. 28408, from upper part of Gering Formation, Banner County, Nebraska. $\times\frac{1}{2}$. (See inferior and superior dentitions, figs. 37–39.)

FIG. 32. Lateral, dorsal, and ventral views of skulls, and mandibular rami: *Pithecistes copei,* new species, holotype, F:A.M. 34483 (combination of both sides), from Monroe Creek Formation, Niobrara County, Wyoming; *P. altageringensis,* new species, holotype, F:A.M. 45638 (lateral view only), from upper part of Gering Formation, Niobrara County, Wyoming, and referred, F:A.M. 45635 (mandibular ramus), from upper part of Gering Formation, Niobrara County, Wyoming; *P. mariae,* new species, holotype, F:A.M. 45633, from deposits approximately equal in age to lower part of Gering Formation, Shannon County, South Dakota; *P. tanneri,* new species, holotype, U.N.S.M. 28451 (skull, combination of both sides), from "Zone D" of Brule Formation, Morrill County, Nebraska; *P. brevifacies* Cope, holotype, A.M. 8129 (mandibular ramus only), from deposits approximately equal in age to upper part of Gering Formation, Montana. $\times\frac{1}{2}$. (See inferior and superior dentitions, figs. 37–39.)

FIG. 33. Lateral, dorsal, and ventral views of skulls, mandibular rami: *Leptauchenia margeryae,* new species, holotype, F:A.M. 45632, and referred, F:A.M. 56831 (dorsal view only, in outline), from Monroe Creek Formation, Niobrara County, Wyoming; *L. parasimus,* new species, holotype, F:A.M. 34485 (skull, lateral view only), and referred, F:A.M. 45639 (mandible only) from upper part of Gering Formation, Niobrara County, Wyoming; *L. decora* Leidy, holotype, A.N.S.P. 10878 (skull, lateral view only), from oreodont faunal "Zone D" of Brule Formation, South Dakota, and referred, F:A.M. 45502 (skull, combination of both sides), from "Zone D" of Brule Formation, Washabaugh County, South Dakota; *L. harveyi,* new species, holotype, U.N.S.M. 28450, from "Zone C" of Brule Formation, Sioux County, Nebraska; *L. martini,* new species, holotype, F:A.M. 45571A, from Gering Formation equivalent, and referred, F:A.M. 45571B, from Washabaugh County, South Dakota. $\times\frac{1}{2}$. (See inferior and superior dentitions, figs. 37–39.)

FIG. 34. Lateral, dorsal, and ventral views of skulls: *Cyclopidius emydinus* Cope, holotype, A.M. 8115, from deposits approximately equal in age to Gering Formation, Montana, and referred, F:A.M. 56960 (mandibular ramus only), from deposits approximately equal in age to Gering Formation, Meagher County, Montana; *C. simus* Cope, holotype, A.M. 8116 (skull only), from deposits approximately equal in age to Gering Formation, Montana.

Mandibular rami: *Cyclopidius simus* Cope, referred, A.M. 8117, from deposits approximately equal in age to Gering Formation, Montana; *Hadroleptauchenia extrema,* new species, referred, F:A.M. 45636 (combination of both sides), from Monroe Creek Formation, Niobrara County, Wyoming; *H. densa* (Loomis), referred, F:A.M. 37525, from upper part of Gering Formation, Niobrara County, Wyoming; *H. shanafeltae,* new species, holotype, U.N.S.M. 1082, from lower part of Gering Formation, Morrill County, Nebraska. $\times\frac{1}{2}$. (See skulls of *Hadroleptauchenia* species, fig. 35; inferior and superior dentitions, figs. 37–39.)

FIG. 35. Lateral, dorsal, and ventral views of skulls: *Hadroleptauchenia extrema,* new species, holotype, F:A.M. 45602 (combination of both sides), from Monroe Creek Formation, Niobrara County, Wyoming; *H. densa* (Loomis), holotype, A.C. 7695 (lateral view only), from upper part of Gering Formation, Goshen County, Wyoming, and referred, F:A.M. 37525, from upper part of Gering Formation, Niobrara County, Wyoming; *H. shanafeltae,* new species, holotype, U.N.S.M. 1082, from lower part of Gering Formation, Morrill County, Nebraska; *H. primitiva,* new species, holotype, F:A.M. 45577, from oreodont faunal "Zone D" of Brule Formation, Washabaugh County, South Dakota; *H. eiseleyi,* new species,

holotype, U.N.S.M. 28208 (lateral view only), from "Zone A" of Brule Formation, Scotts Bluff County, Nebraska. ×½. (See mandibular rami of *Hadroleptauchenia* species, fig. 34; inferior and superior dentitions, figs. 37–39.)

FIG. 36. Lateral and dorsal views of skulls: *Pseudocyclopidius lullianus expiratus,* new subspecies, holotype, F:A.M. 45598, from Monroe Creek Formation, Converse County, Wyoming; *P. lullianus* (Thorpe), referred, F:A.M. 45597, from upper part of Gering Formation, Niobrara County, Wyoming; *P. major* (Leidy), holotype, A.N.S.P. 10941 (lateral view only), from deposits approximately equal in age to lower part of Gering Formation, Morrill County, Nebraska, and referred, U.N.S.M. 1080 and 1081, from lower part of Gering Formation, Morrill County, Nebraska; *P. frankforteri,* new species, holotype, F:A.M. 45500 (combination of both sides), from oreodont faunal "Zone D" of Brule Formation, Shannon County, South Dakota; *P. orellaensis,* new species, holotype, F:A.M. 45528 (lateral view only), from "Zone A" of Brule Formation, Converse County, Wyoming. ×½. See skull and mandibles, fig. 35; inferior and superior dentitions, figs. 37–39.)

FIG. 37. Ventral views of skulls, and mandibular rami: *Pseudocyclopidius lullianus expiratus,* new subspecies, holotype, F:A.M. 45598, and referred, F:A.M. 45601, from Monroe Creek Formation, Converse County, Wyoming; *P. lullianus* (Thorpe, referred, F:A.M. 45597 (skull) and F:A.M. 34484 (mandible), from upper part of Gering Formation, Niobrara County, Wyoming; *P. major* (Leidy), referred, U.N.S.M. 1080 (combination of both sides) and 1081, from lower part of Gering Formation, Morrilll County, Nebraska; *P. frankforteri,* new species, holotype, F:A.M. 45500 (skull, combination of both sides), from oreodont faunal "Zone D" of Brule Formation, Shannon County, South Dakota; *P. orellaensis,* new species, holotype, F:A.M. 45528 (skull only), from "Zone A" of Brule Formation, Converse County, Wyoming, and referred (mandibular rami only), F:A.M. 45637 (combination of both sides), from "Zone A" of Brule Formation, Converse County, Wyoming, and U.N.S.M. 28230, from "Zone A" of Brule Formation, Sioux County, Nebraska. ×½. (See skull, fig. 36; inferior and superior dentitions, figs. 37–39.)

FIG. 38. Superior dentitions: *Sespia ultima,* new species, holotype, F:A.M. 45606, from Monroe Creek Formation, Niobrara County, Wyoming; *S. heterodon* (Cope), holotype, A.M. 8131, from deposits approximately equal in age to Gering Formation, Montana; *S. nitida* (Leidy), holotype, A.N.S.P. 10870, from deposits ?equal in age to upper part of Gering Formation, South Dakota, referred, F:A.M. 45622, from upper part of Gering Formation, Laramie County, Wyoming, and F:A.M. 45611A, from upper part of Gering Formation, Niobrara County, Wyoming; *S. californica* (Stock), holotype, U.C. 27720, from deposits approximately equal in age to Gering Formation, Ventura County, California; *S. marianae,* new species, holotype, U.N.S.M. 28420A, from lower part of Gering Formation, Morrill County, Nebraska; *Megasespia middleswarti,* new species, holotype, U.N.S.M. 28408, from upper part of Gering Formation, Banner County, Nebraska; *Pithecistes copei,* new species, holotype, F:A.M. 34483 (combination of both sides), from Monroe Creek Formation, Niobrara County, Wyoming; *P. altageringensis,* new species, holotype, F:A.M. 45638, from upper part of Gering Formation, Niobrara County, Wyoming; *P. mariae,* new species, holotype, F:A.M. 45633, from deposits approximately equal in age to lower part of Gering Formation, Shannon County, South Dakota; *P. tanneri,* new species, holotype, U.N.S.M. 28451, from oreodont faunal "Zone D" of Brule Formation, Morrill County, Nebraska; *Cyclopidius emydinus* Cope, holotype, A.M. 8115, from deposits approximately equal in age to Gering Formation, Montana; *C. simus* Cope, holotype, A.M. 8116, from deposits approximately equal in age to Gering Formation, Montana; *Leptauchenia margeryae,* new species, holotype, F:A.M. 45632, from Monroe Creek Formation, Niobrara County, Wyoming; *L. parasimus,* new species, holotype, F:A.M. 34485, from upper part of Gering Formation, Niobrara County, Wyoming; *L. martini,* new species, holotype, F:A.M. 45571A, from "Zone D" of Brule Formation, Washabaugh County, South Dakota; *L. decora* Leidy, holotype, A.N.S.P. 10878, from "Zone D" of Brule Formation, South Dakota, and referred, F:A.M. 45502, from "Zone D" of Brule Formation, Washabaugh County, South Dakota; *L. harveyi,* new species, holotype, U.N.S.M. 28450, from "Zone C" of Brule Formation, Sioux County, Nebraska; *Hadroleptauchenia extrema,* new species, holotype, F:A.M. 45602, from Monroe Creek Formation, Niobrara County, Wyoming; *H. densa* (Loomis), referred, F:A.M. 37525, from upper part of Gering Formation, Goshen County, Wyoming; *H. shanafeltae,* new species, holotype, U.N.S.M. 1082, from lower part of Gering Formation, Morrill County, Nebraska; *H. primitiva,* new species, holotype, F:A.M. 45577, "Zone D" of Brule Formation, Washa-

baugh County, South Dakota; *H. eiseleyi,* new species, holotype, U.N.S.M. 28208, from "Zone A" of Brule Formation, Scotts Bluff County, Nebraska. Natural size. (See inferior dentitions, fig. 40.)

FIG. 39. Superior dentitions: *Pseudocyclopidius lullianus expiratus,* new subspecies, holotype, F:A.M. 45598, and referred, F:A.M. 45601, from upper part of Gering Formation, Niobrara County, Wyoming; *P. lullianus* (Thorpe), referred, F:A.M. 45597, from upper part of Gering Formation, Niobrara County, Wyoming; *P. major* (Leidy), holotype, A.N.S.P. 10941, and referred, A.N.S.P. 10940, from deposits approximately equal in age to lower part of Gering Formation, South Dakota, and referred, U.N.S.M. 1080, from lower part of Gering Formation, Morrill County, Nebraska; *P. frankforteri,* new species, holotype, F:A.M. 45500, from oreodont faunal "Zone D" of Brule Formation, Shannon County, South Dakota; *P. orellaensis,* new species, holotype, F:A.M. 45528, from "Zone A" of Brule Formation, Converse County, Wyoming; *Sespia ultima,* new species, holotype, F:A.M. 45606, from Monroe Creek Formation, Niobrara County, Wyoming; *S. heterodon* (Cope), holotype, A.M. 8131, from deposits approximately equal in age to Gering Formation, Montana; *Hadroleptauchenia densa* (Loomis), holotype, A.C. 7695, from upper part of Gering Formation, Goshen County, Wyoming (see inferior dentition, same fig.)

Mandibular rami and inferior dentitions: *Sespia ultima,* new species, holotype, F:A.M. 45606, from Monroe Creek Formation, Niobrara County, Wyoming; *S. heterodon* (Cope), holotype, A.M. 8131, from deposits approximately equal in age to Gering Formation, Montana; *S. marianae,* new species, holotype, U.N.S.M. 28420A, from lower part of Gering Formation, Morrill County, Nebraska; *Hadroleptauchenia densa* (Loomis), holotype, A.C. 7695, from upper part of Gering Formation, Goshen County, Wyoming (see superior series, same fig.). Natural size.

FIG. 40. Inferior dentitions: *Sespia ultima,* new species, holotype, F:A.M. 45606, from Monroe Creek Formation, Niobrara County, Wyoming; *S. nitida* (Leidy), referred, F:A.M. 45611A, from upper part of Gering Formation, Niobrara County, Wyoming; *S. californica* (Stock), holotype, U.C. 27720, from deposits approximately equal in age to Gering Formation, Ventura County, California; *S. marianae,* new species, holotype, U.N.S.M. 28420A, from lower part of Gering Formation, Morrill County, Nebraska; *Megasespia middleswarti,* new species, holotype, U.N.S.M. 28408, from upper part of Gering Formation, Banner County, Nebraska; *Pithecistes brevifacies* Cope, holotype, A.M. 8129, from deposits approximately equal in age to Gering Formation, Montana; *P. copei,* new species, holotype, F:A.M. 34483, from Monroe Creek Formation, Niobrara County, Wyoming; *P. altageringensis,* new species, referred, F:A.M. 45635, from upper part of Gering Formation, Niobrara County, Wyoming; *P. mariae,* new species, holotype, F:A.M. 45633, from deposits approximately equal in age to lower part of Gering Formation, Shannon County, South Dakota; *P. tanneri,* new species, holotype, U.N.S.M. 28451, from oreodont faunal "Zone D" of Brule Formation, Morrill County, Nebraska; *Cyclopidius emydinus* Cope, referred, F:A.M. 56960, from deposits approximately equal in age to Gering Formation, Meagher County, Montana; *C. simus* Cope, referred, A.M. 8117, from deposits approximately equal in age to Gering Formation, Montana; *Leptauchenia margeryae,* new species, holotype, F:A.M. 45632, from Monroe Creek Formation, Niobrara County, Wyoming; *L. parasimus,* new species, referred, F:A.M. 45639, from upper part of Gering Formation, Niobrara County, Wyoming; *L. martini,* new species, referred, F:A.M. 45571B, from deposits equivalent to Gering Formation, Washabaugh County, South Dakota; *L. decora* Leidy, referred, F:A.M. 45502, from "Zone D" of Brule Formation, Washabaugh County, South Dakota; *L. harveyi,* new species, holotype, U.N.S.M. 28450, from "Zone C" of Brule Formation, Sioux County, Nebraska; *Hadroleptauchenia extrema,* new species, referred, F:A.M. 45636, from Monroe Creek Formation, Niobrara County, Wyoming; *H. densa* (Loomis) referred, F:A.M. 37525, from upper part of Gering Formation, Goshen County, Wyoming; *H. shanafeltae,* new species, holotype, U.N.S.M. 1082, from lower part of Gering Formation, Morrill County, Nebraska; *Pseudocyclopidius lullianus expiratus,* new subspecies, holotype, F:A.M. 45598, and referred, F:A.M. 45601, from Monroe Creek Formation, Converse County, Wyoming; *P. lullianus* (Thorpe), referred, F:A.M. 34484, from upper part of Gering Formation, Niobrara County, Wyoming; *P. major* (Leidy), referred, U.N.S.M. 1080 and 1081, from lower part Gering Formation, Morrill County, Nebraska; *P. frankforteri,* new species, holotype, F:A.M. 45500, from "Zone D" of Brule Formation, Shannon County, South Dakota; *P. orellaensis,* new species, referred, U.N.S.M. 28230, from

"Zone A" of Brule Formation, Sioux County, Nebraska, and F:A.M. 45637, from "Zone A" of Brule Formation, Converse County, Wyoming. Natural size.

FIG. 41. Occipital regions of skulls: *Sespia marianae,* new species, holotype, U.N.S.M. 28420A, from lower part of Gering Formation, Morrill County, Nebraska; *Leptauchenia decora* Leidy, referred, F:A.M. 45502, from oreodont faunal "Zone D" of Brule Formation, Washabaugh County, South Dakota; *Cyclopidius emydinus* Cope, holotype, A.M. 8115, from deposits approximately equal in age to Gering Formation, Montana; *Pseudocyclopidius major* (Leidy), referred, U.N.S.M. 1080, from lower part of Gering Formation, Morrill County, Nebraska. Natural size.

FIG. 42. Mandibular rami: *Sespia ultima,* new species, holotype, F:A.M. 45606, from Monroe Creek Formation, Niobrara County, Wyoming, compared with a recent *Equus hemionus.* The most hypsodont molar teeth of the oreodonts are enlarged to the size of those of recent horse, indicating that proportionately the M_3 in the mandible of *Sespia* is more hypsodont than the lower molars of the horse (*Equus*).

FIG. 43. Comparison of limb elements: A, *Sespia marianae,* new species; B, *S. nitida* (Leidy); C, *Megasespia middleswarti,* new species; D, *Leptauchenia decora* Leidy; E, *Hadroleptauchenia shanafeltae,* new species; F, *Pseudocyclopidius major* (Leidy); G, *P. lullianus expiratus,* new subspecies; H, *P. lullianus* (Thorpe); I, *P. orellaensis.* $\times\frac{1}{2}$.

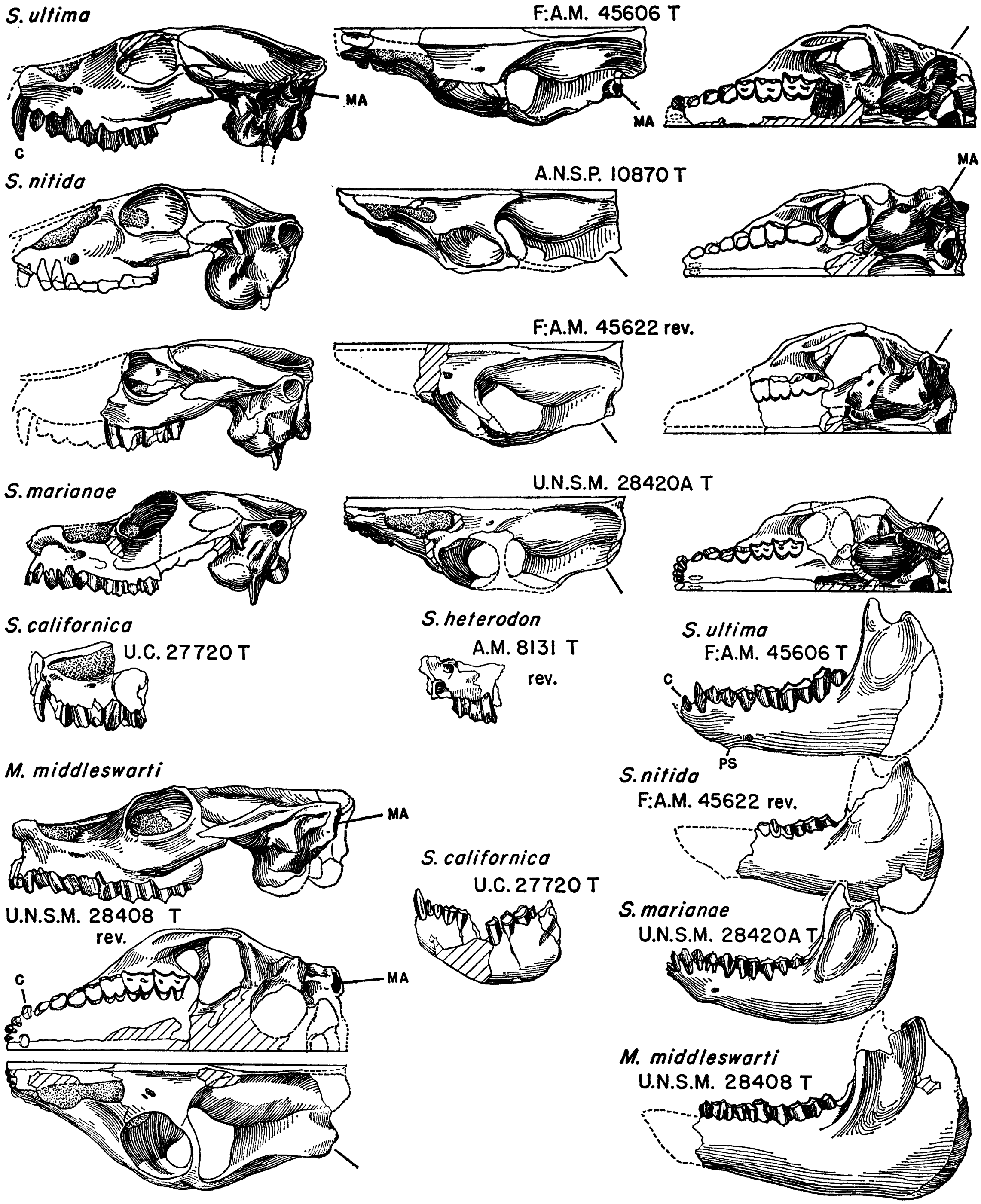


FIG. 31. *Sespia,* five species, holotypes, A.N.S.P. 10870, F:A.M. 45606, A.M. 8131, U.C. 27720, and U.N.S.M. 28420A, and referred, F:A.M. 45622; *Megasespia,* one species, holotype, U.N.S.M. 28408. (See p. 346.) $\times\frac{1}{2}$.

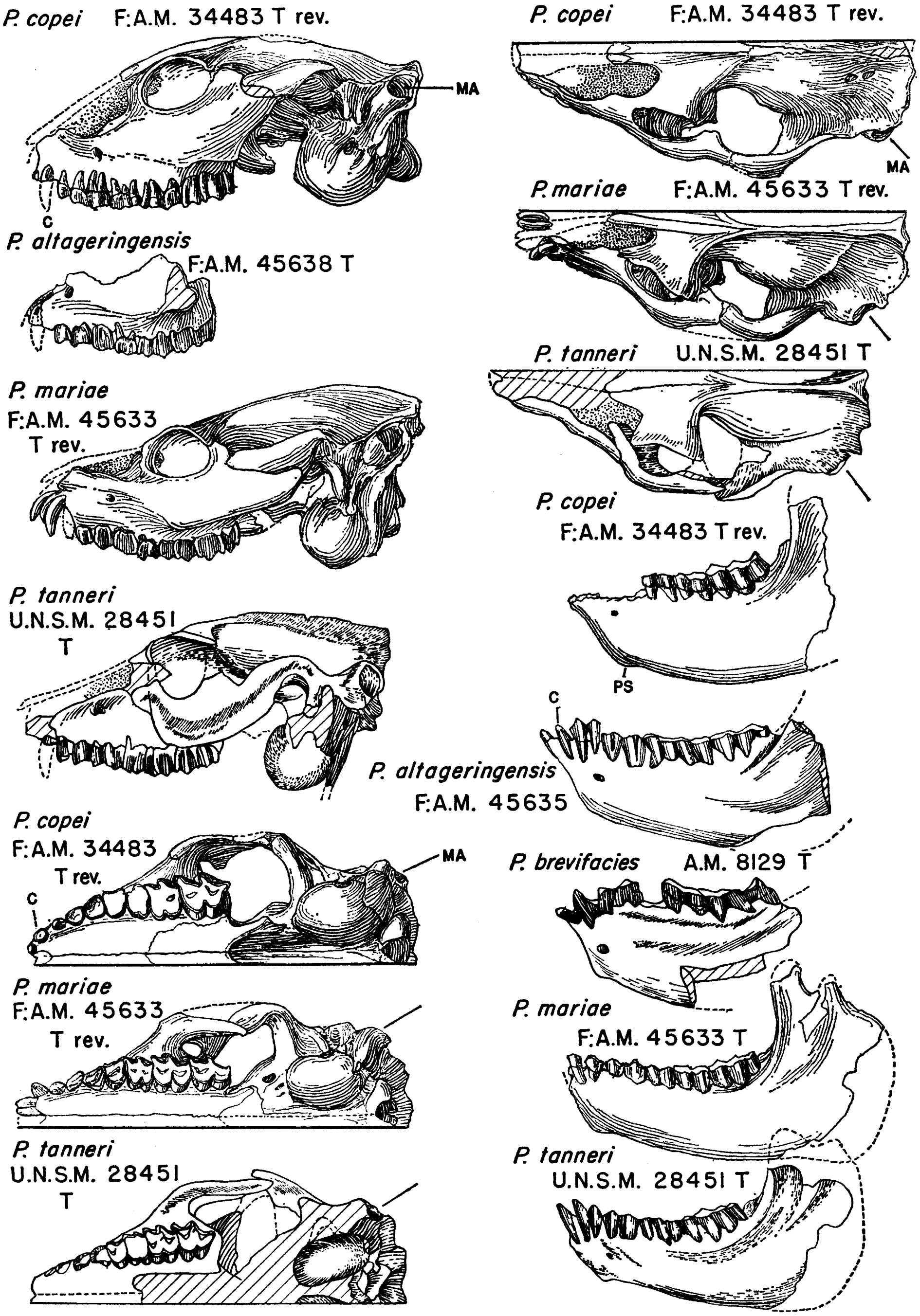


FIG. 32. *Pithecistes,* five species, holotypes, A.M. 8129, F:A.M. 34483, 45638, 45633, and U.N.S.M. 28451, and referred, F:A.M. 45635. (See p. 346.) $\times\frac{1}{2}$.

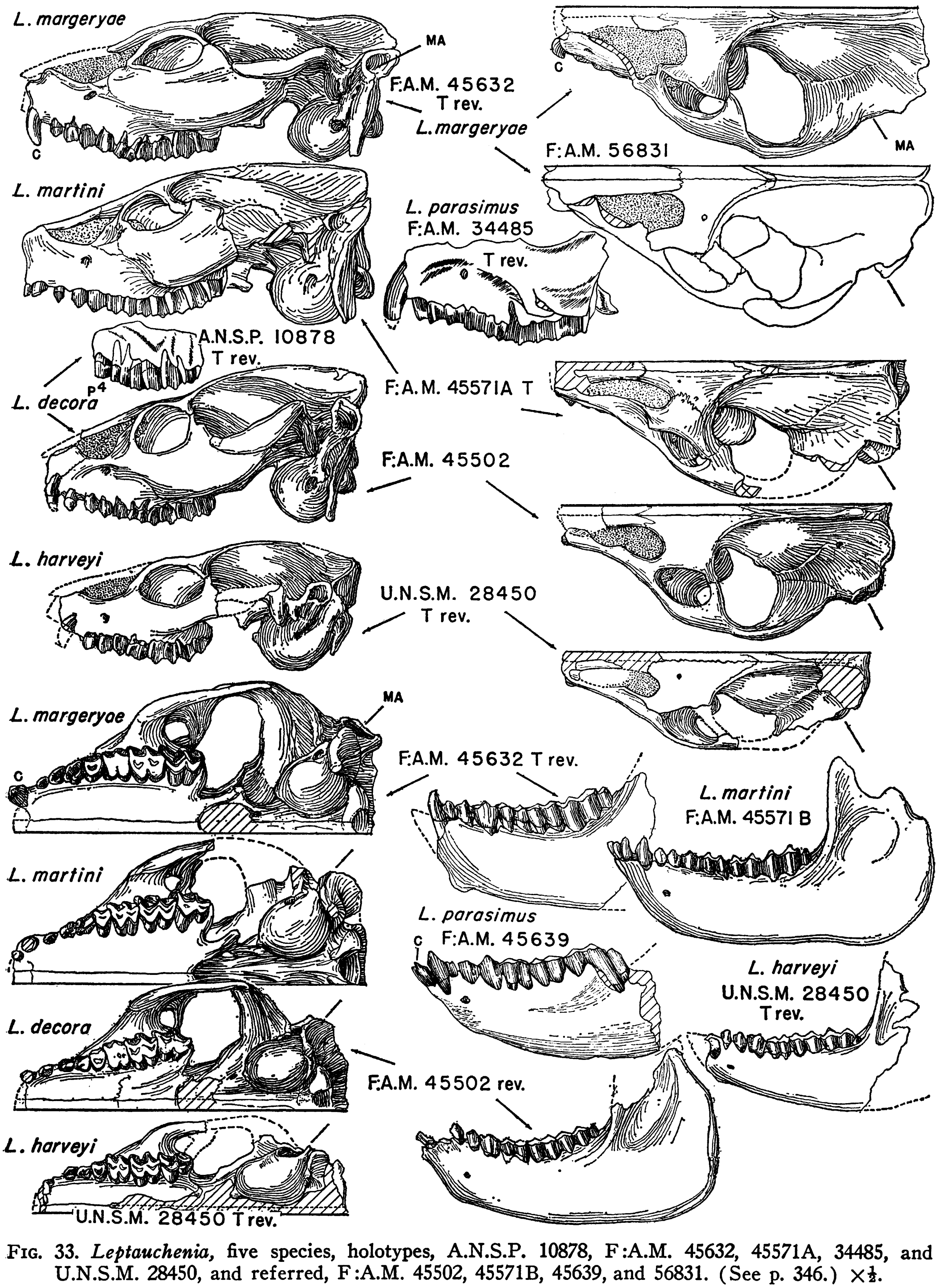


FIG. 33. *Leptauchenia,* five species, holotypes, A.N.S.P. 10878, F:A.M. 45632, 45571A, 34485, and U.N.S.M. 28450, and referred, F:A.M. 45502, 45571B, 45639, and 56831. (See p. 346.) ×½.

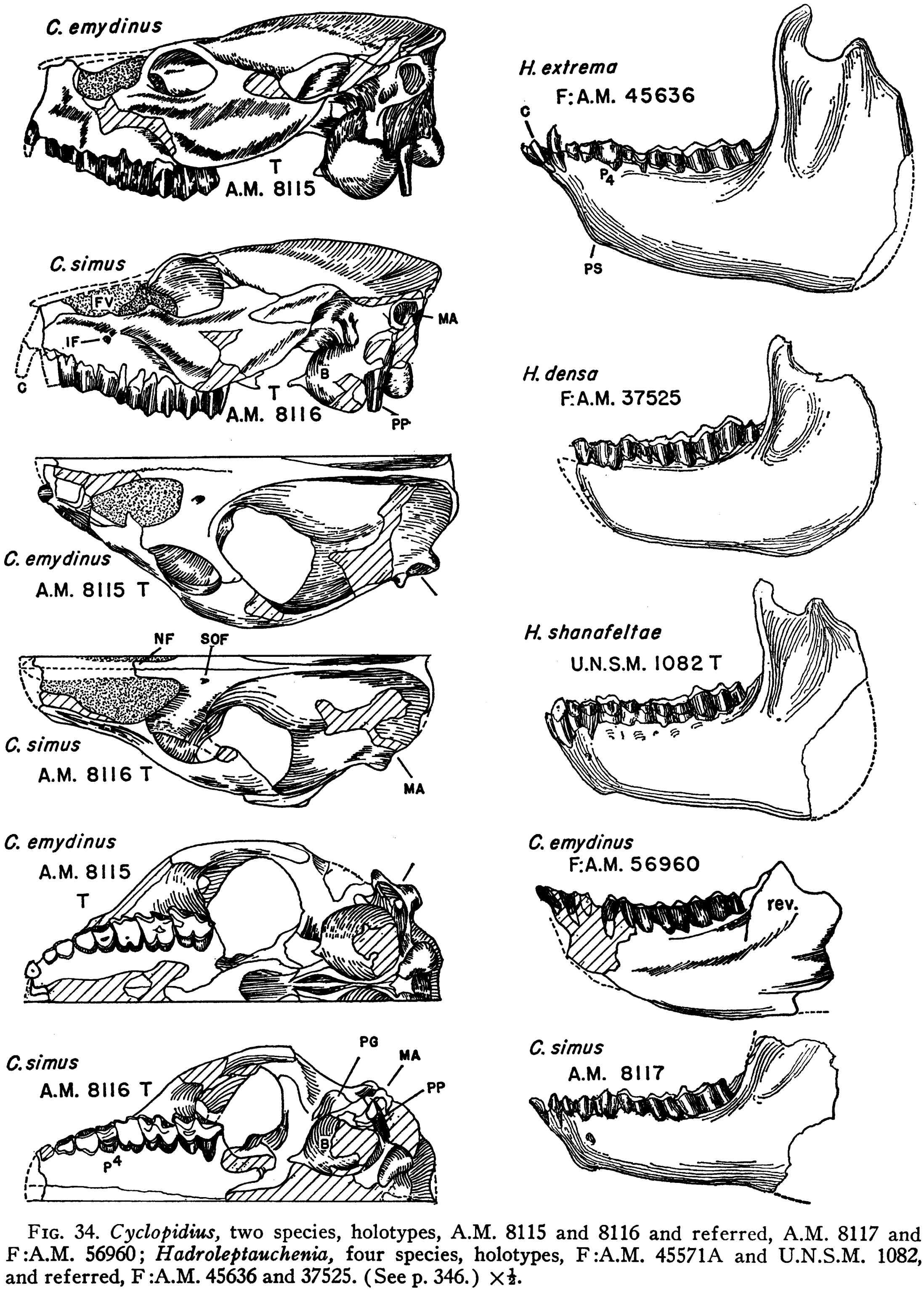


FIG. 34. *Cyclopidius,* two species, holotypes, A.M. 8115 and 8116 and referred, A.M. 8117 and F:A.M. 56960; *Hadroleptauchenia,* four species, holotypes, F:A.M. 45571A and U.N.S.M. 1082, and referred, F:A.M. 45636 and 37525. (See p. 346.) ×½.

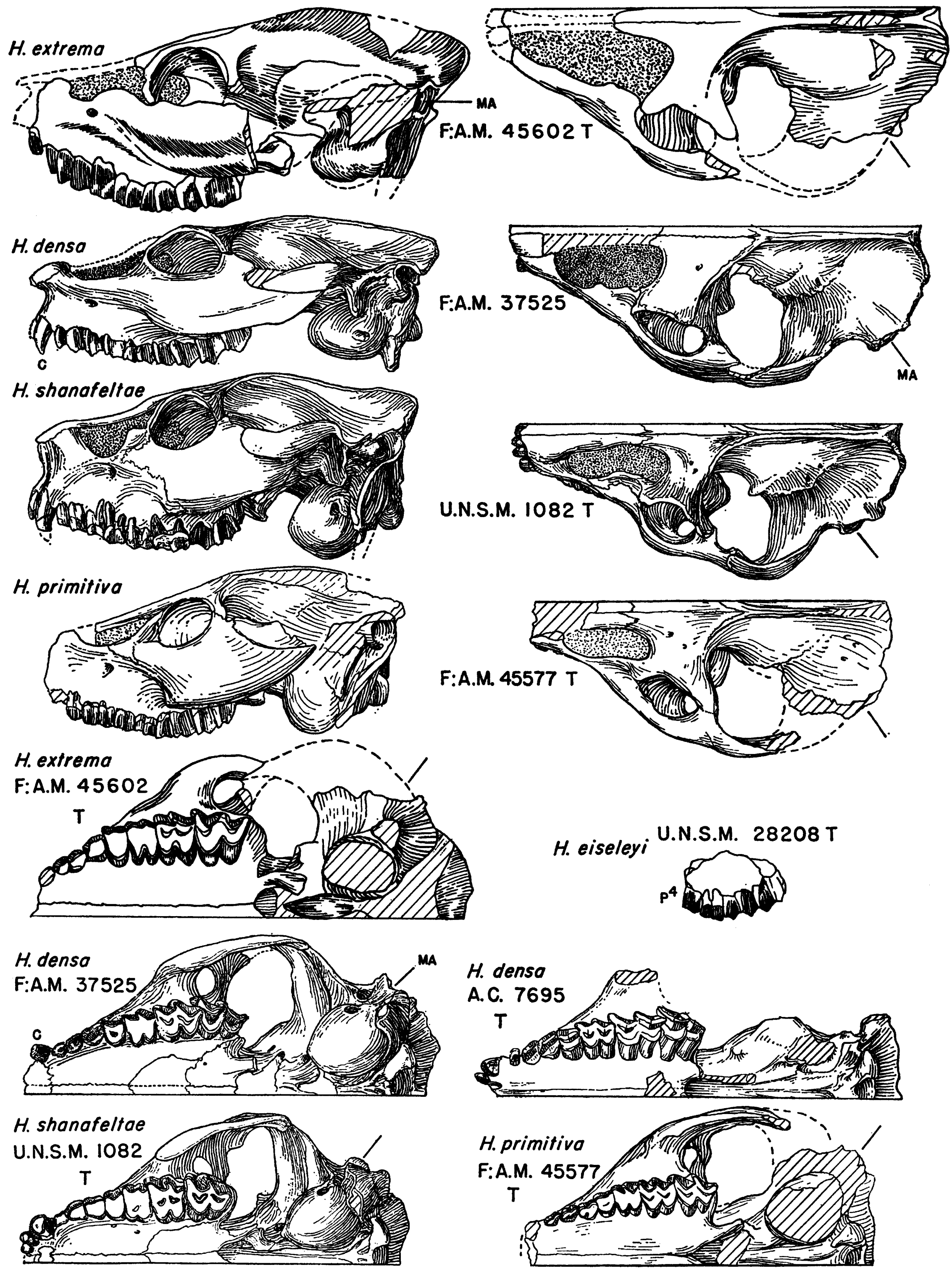


FIG. 35. *Hadroleptauchenia,* five species, holotypes, A.C. 7695, F:A.M. 45602 and 45577, and U.N.S.M. 1082 and 28308, and referred, F:A.M. 37525. (See p. 346.) ×½.

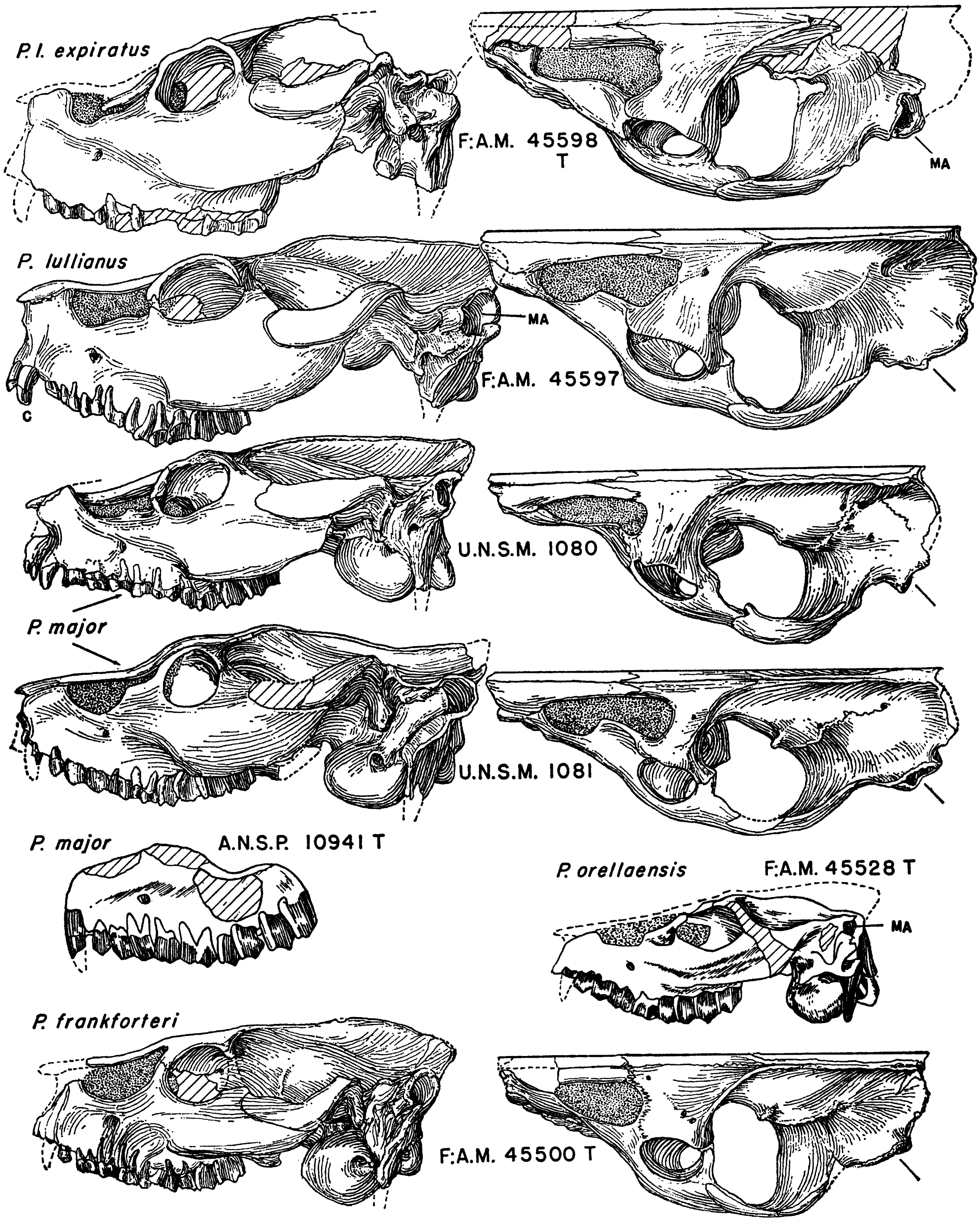


FIG. 36. *Pseudocyclopidius,* four species and one subspecies, holotypes, A.N.S.P. 10941, F:A.M. 45598, 45528, and 45500, and referred, F:A.M. 45597, and U.N.S.M. 1080 and 1081. (See p. 347.) ×½.

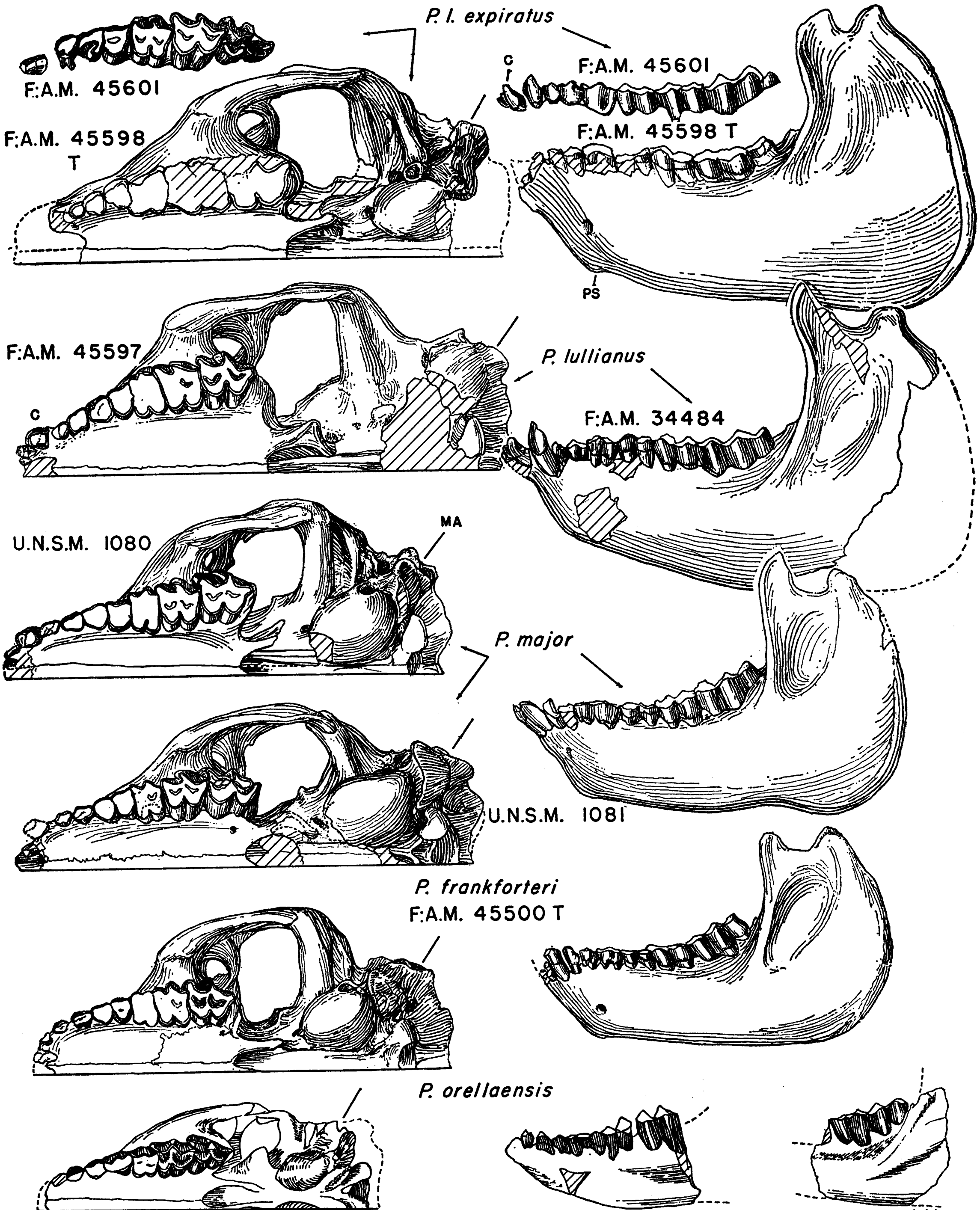


FIG. 37. *Pseudocyclopidius,* four species and one subspecies, holotypes, F:A.M. 45598, 45500, 45528, and U.N.S.M. 45528, and referred, F:A.M. 45601, 45597, 34484, 45637, and U.N.S.M. 1080, 1081, and 28230. (See p. 347.) ×½.

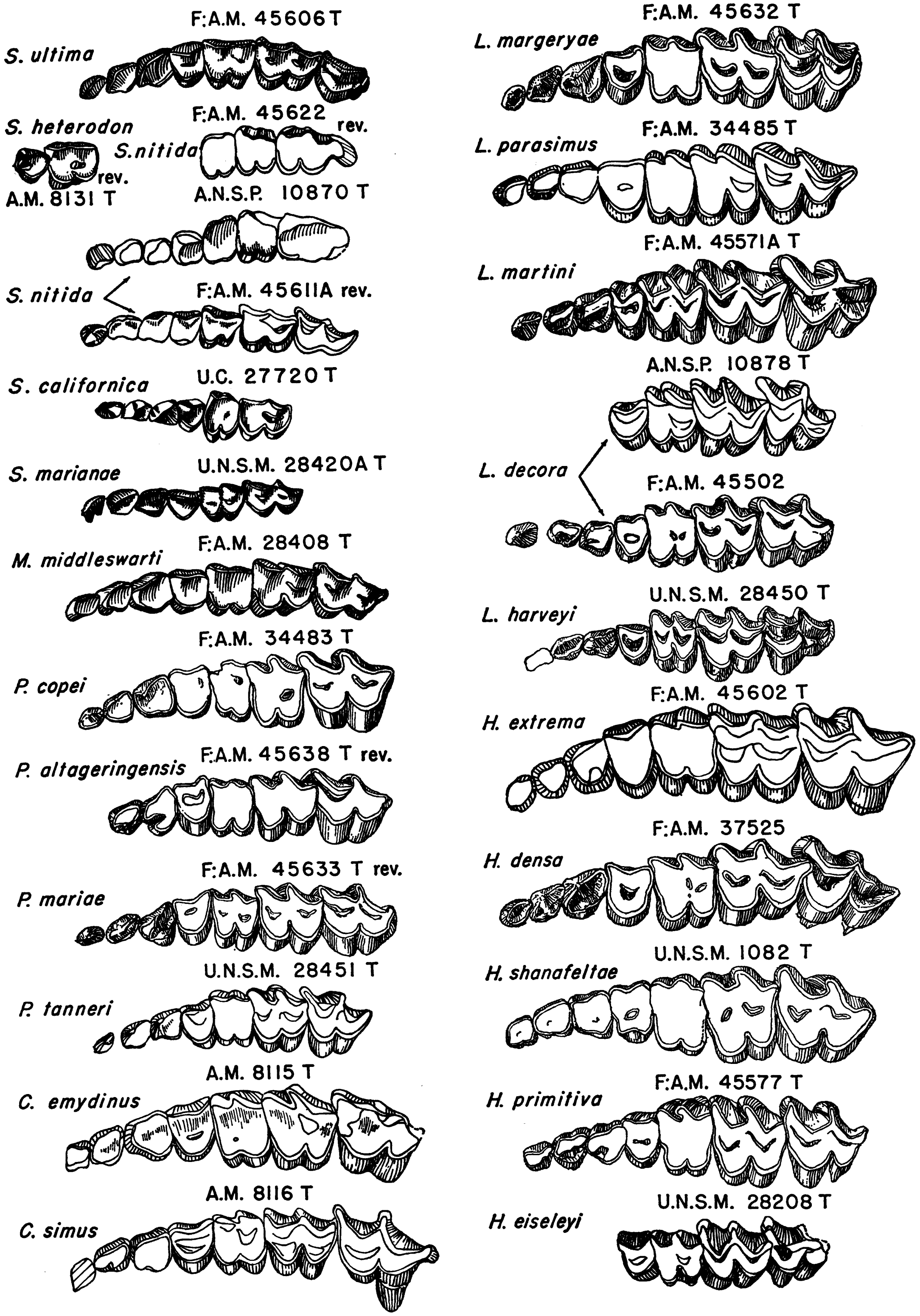


FIG. 38. *Sespia,* six species, five holotypes (T), and two referred; *Megasespia,* one species, holotype; *Pithecistes,* four species, four holotypes; *Cyclopidius,* two species, two holotypes; *Leptauchenia,* five species, five holotypes and one referred; *Hadroleptauchenia,* five species, four holotypes and one referred. (See p. 347.) $\times 1$.

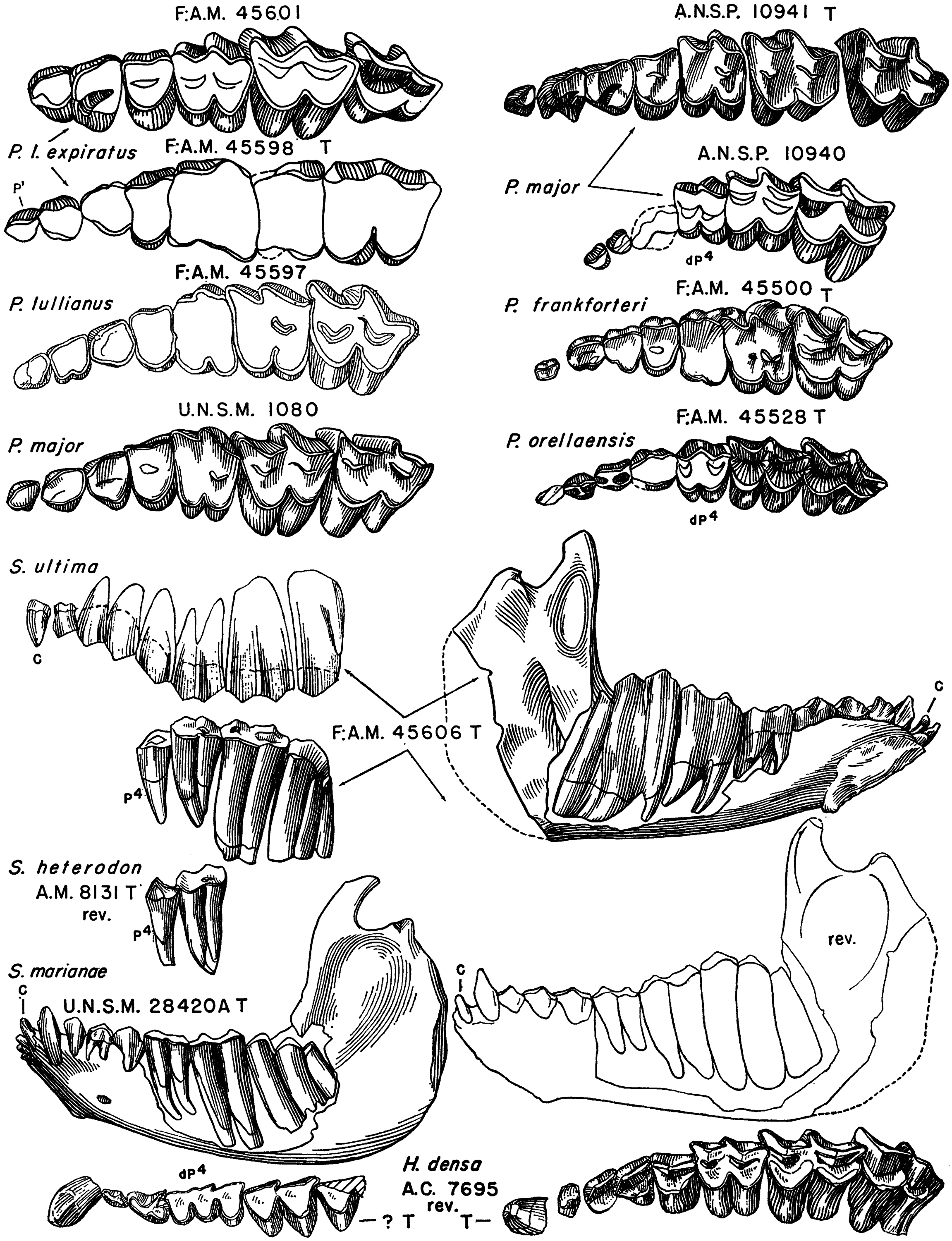


FIG. 39. *Pseudocyclopidius*, five species, three holotypes (T), and four referred; *Sespia*, three species, three holotypes; *Hadroleptauchenia*, one species, holotype. (See p. 348.) ×1.

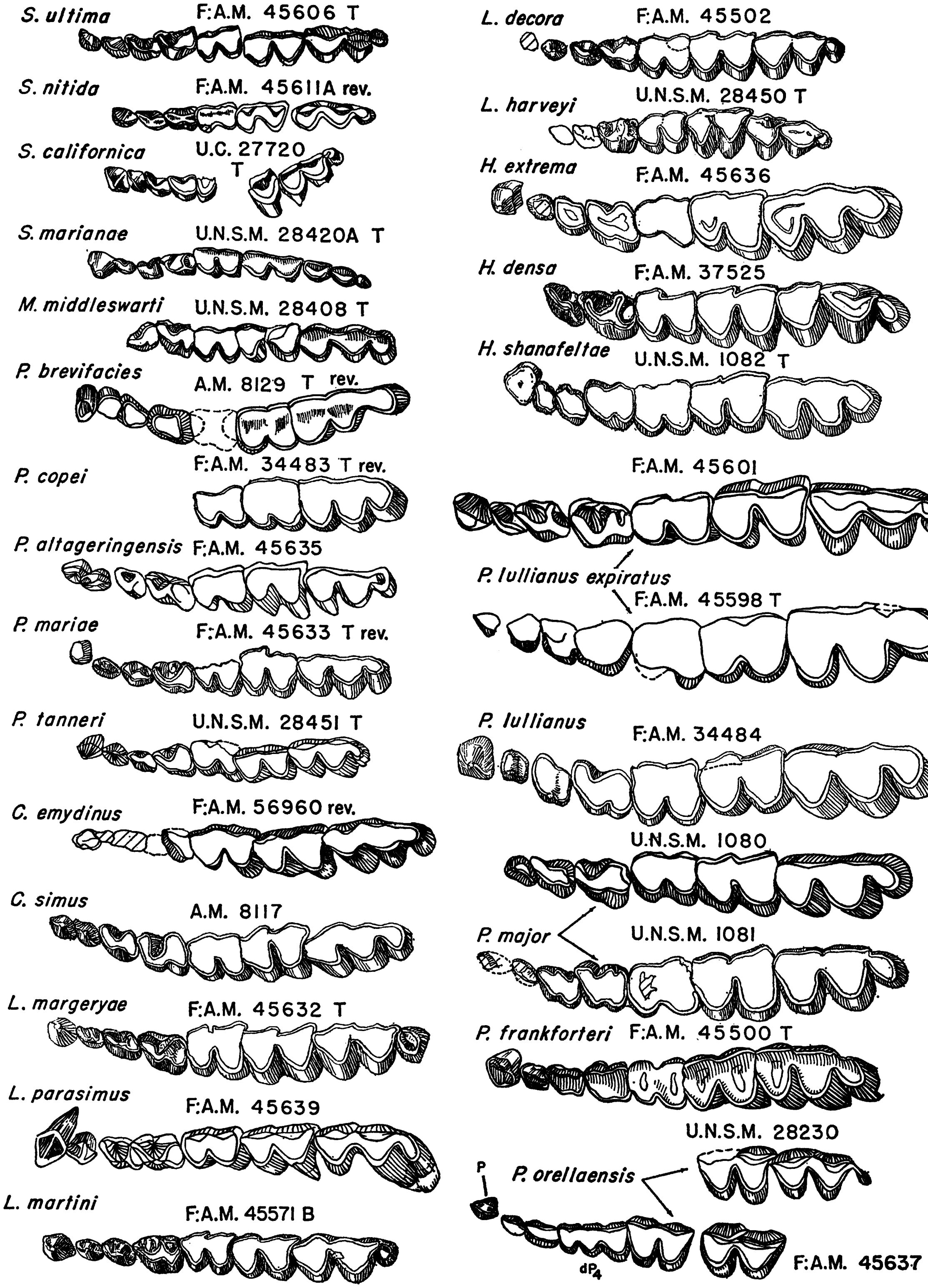


FIG. 40. *Sespia,* four species, three holotypes (T), and one referred; *Megasespia,* one species, holotype; *Pithecistes,* four species, four holotypes, and one referred; *Cyclopidius,* two species, two holotypes; *Leptauchenia,* five species, three holotypes, and two referred; *Hadroleptauchenia,* three species, two holotypes, and two referred; *Pseudocyclopidius,* four species and one subspecies, two holotypes, and six referred. (See p. 348.) ×1.

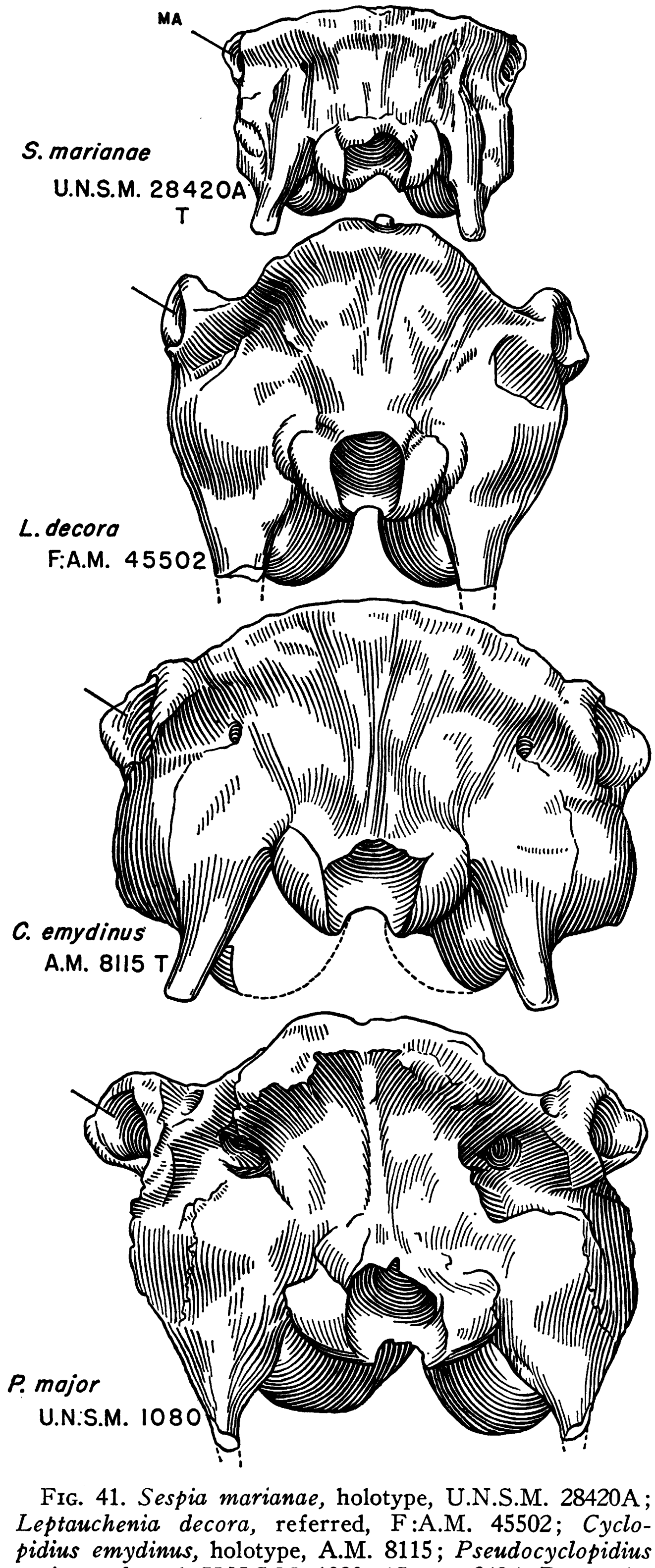


FIG. 41. *Sespia marianae,* holotype, U.N.S.M. 28420A; *Leptauchenia decora,* referred, F:A.M. 45502; *Cyclopidius emydinus,* holotype, A.M. 8115; *Pseudocyclopidius major,* referred, U.N.S.M. 1080. (See p. 349.) Drawn by Robert Miller. ×1.

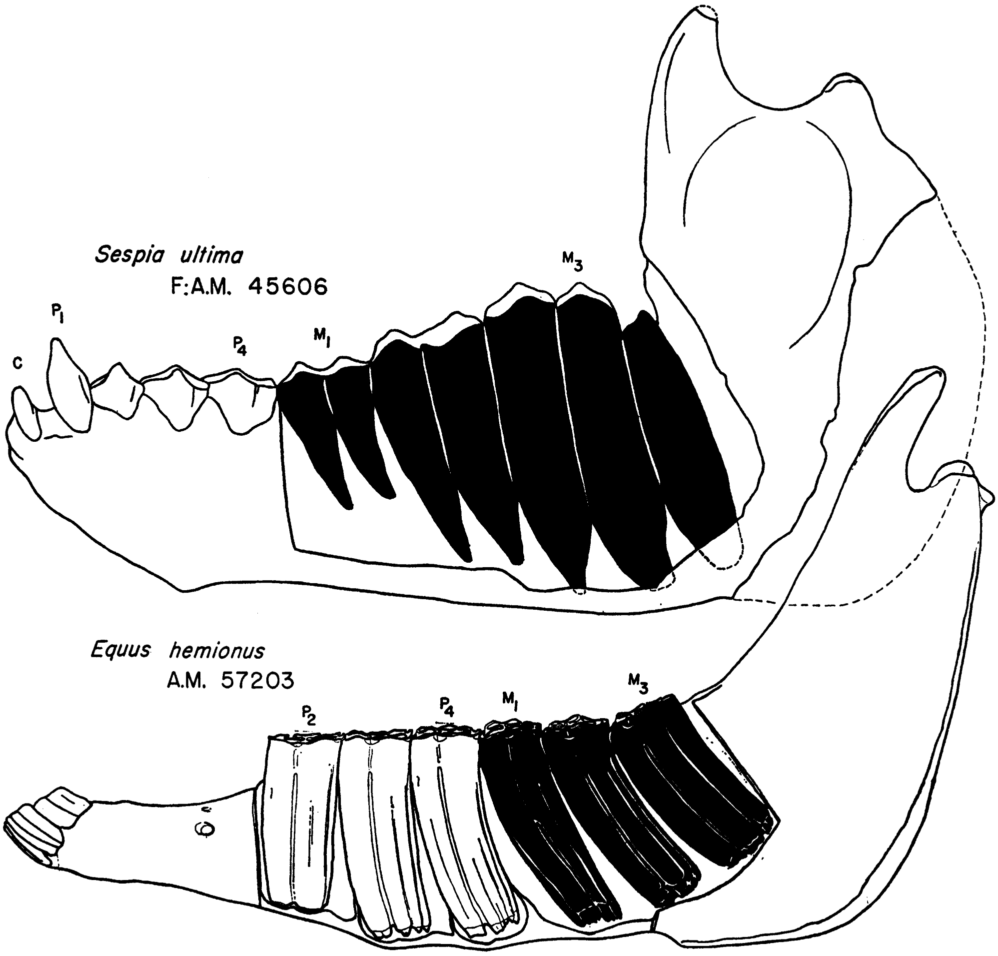


FIG. 42. *Sespia ultima,* holotype, F:A.M. 45606; *Equus hemionus,* referred, A.M. 57203. (See p. 349.) *Sespia,* ×½ (approximately); *Equus,* ×⅓ (approximately).

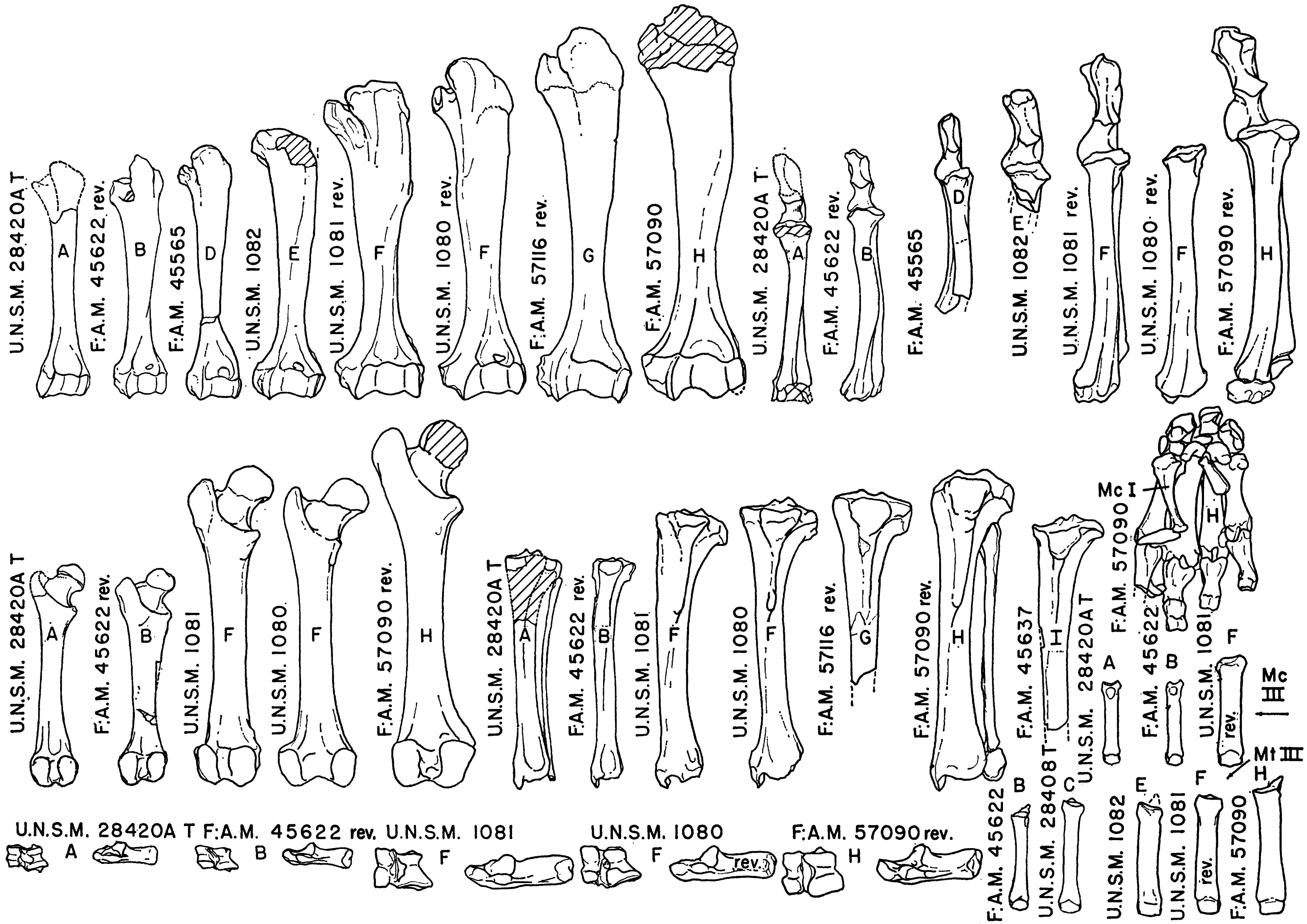


FIG. 43. Comparison of limb elements: A, *Sespia marianae;* B, *S. nitida;* C, *Megasespia middle swarti;* D, *Leptauchenia decora;* E, *Hadroleptauchenia shanafeltae;* F, *Pseudocyclopidius major;* G, *P. l. expiratus;* H, *P. lullianus;* I, *P. orellaensis.* (See p. 349.) ×½.

APPENDIX TO SIX SUBFAMILIES OF THE MERYCOIDODONTIDAE

THE FOLLOWING LISTED NEW MATERIAL and observations represent an appendix to the revision of the Merycoidodontidae. These new data have not resulted in any significant changes in the conclusions on the previously published subfamilies. Some of the additional specimens, however, have provided supplemental information regarding specific characters and geographic distribution of the oreodonts.

Numerous new examples of *Bathygenys alpha* have demonstrated the possible range in individual variation in this species. Two new genera of the Oreonetinae, *Megabathygenys* and *Parabathygenys,* are described in the Appendix. This new information adds greatly to the knowledge of the oreodonts from faunal "Zone B" of the Chadron. Much of the previously known oreodont material from the middle part of the Chadron has been fragmentary.

Included in the additional material are specimens that increase the knowledge and distribution of *Brachycrus, Ustatochoerus, Ticholeptus, Merychyus, M.* (*Metoreodon*), *Desmatochoerus, D.* (*Paradesmatochoerus*), and the Miniochoerinae.

The discussion of *Ustatochoerus* (p. 373) includes a comparison of the geologic occurrences of the oreodonts from the Texas Gulf Coast region and those of the central Great Plains.

CHART 11

SIZE RANGE IN THE MERYCOCHOERINAE[a]

	No. of Examples	Skull Basal Length		Dentition P^1–M^3		Dentition P_1–M_3	
		Range	Mean	Range	Mean	Range	Mean
I. *Brachycrus*							
B. buwaldi, = "Sheep Creek" (Calif.)	107[b]	246	246	129	129	125	125
B. b. barstowensis, = "Sheep Creek" (Calif.)	6	—	—	123	123	117	117
B. altiramus, = "lower Snake Creek" (Mont.)	1	302	302	155	155	158	158
B. laticeps, = "lower Snake Creek" (Mont.)	2	242	242	142	142	151	151
B. siouense, "lower Snake Creek" (Nebr.)	516	222–255	234	114–132	120	111–141	130.5
B. wilsoni, "Sheep Creek" (Nebr.)	96	270–275	272.5	126–142	135.5	137–152.5	143.5
B. w. longensis, "Sheep Creek" (Nebr.)	1	—	—	127	127	—	—
B. rusticus, = "Sheep Creek" (Wyo.)	19	—	—	105–110	107.7	111–116	113.5
B. sweetwaterensis, = "lower Snake Creek" (Wyo.)	16	247–259	253	130–141	135	132–149	143.5
B. vaughani, = "lower Snake Creek" (Wyo.)	21	232–252	245	120–128.5	124	125–135	129
II. *Merycochoerus*							
M. proprius, upper Marsland (Nebr.)	93	260–330	292.5	135–172	152	144–178	166
M. p. magnus, upper Marsland (Nebr., Colo.)	18	230–306	268.5	135–161	144	143–173	152
M. matthewi, lower Marsland (S. Dak., Wyo., Nebr.)	19	247–280	268.5	127–155	146	147–165	157

[a] All measurements in millimeters.

[b] In all instances the number of examples is total, but many have no measurement cited, especially in *B. buwaldi,* of which the material is distorted by crushing.

CHART 12

Size Range in the Ticholeptinae[a]

	No. of Examples	Skull Basal Length		Dentition P^1–M^3		Dentition P_1–M_3	
		Range	Mean	Range	Mean	Range	Mean
I. *Ustatochoerus*							
U. californicus raki, = middle Ash Hollow (N. Mex.)	1	—	—	—	—	169	169
U. compressidens, = lower Ash Hollow (Mont.)	1	—	—	—	—	135	135
U. major, middle Ash Hollow (Nebr.)	70	272–288.5	280.5	135–148	141	139–155	147
U. m. texanus, = middle Ash Hollow (Tex.)	2	—	—	—	—	161	161
U. medius, Valentine (Nebr., Colo., Kan.)	88	202–227	216	106–114.5	110.5	114–124.5	116
U. m. mohavensis, = Valentine (Calif.)	1	—	—	113	113	—	—
U. m. novomexicanus, = Valentine (N. Mex.)	50	210–236	226	106.5–122.5	116.5	114–132	123.5
U. profectus, lower Ash Hollow (Nebr., S. Dak., Kan.)	75	236–248	242.5	113–132	124.9	111.5–138	128
U. p. espanolensis, = lower Ash Hollow (N. Mex.)	12	—	—	127–130	128.5	—	—
U. p. studeri, = lower Ash Hollow (Tex.)	17	230	230	113–129	118.5	122–126	124
U. skinneri, middle Ash Hollow (S. Dak., Nebr., Kan.)	6	233–260	246.5	133–140	136.5	145.5–151	148.5
U. s. santacruzensis, = middle Ash Hollow (N. Mex.)	6	—	—	138–150	144	146	146
?*U. schrammi*, Valentine (Nebr., Colo.)	4	—	—	—	—	108	108
II. *Ticholeptus*							
T. calimontanus, = "lower Snake Creek" (Calif.)	4	—	—	—	—	81.9	81.9
T. hypsodus, "lower Snake Creek" (Nebr.)	133	189	189	87.5–99.5	93	96–109	99.5
T. obliquidens, = "lower Snake Creek" (Oreg.)	1	—	—	—	—	99	99
T. rileyi, = "lower Snake Creek" (Tex.)	1	—	—	—	—	96.5	96.5
T. tooheyi, "Sheep Creek" (Nebr.)	1	—	—	86	86	92	92
T. zygomaticus, = "lower Snake Creek" (Mont.)	4	207–210	203.5	95–95.5	95.2	102.5	102.5
T. z. smithi, = "lower Snake Creek" (Mont.)	1	179	179	87.5	87.5	—	—
III. *Mediochoerus*							
M. blicki, "lower Snake Creek" (Nebr.)	3	182	182	102–103.5	102.7	—	—
M. johnsoni, upper Marsland (Nebr.)	1	195	195	89.5	89.5	—	—

[a] All measurements in millimeters.

TABLE 16

Brachycrus Matthew, *Ustatochoerus* Schultz and Falkenbach, *Ticholeptus* Schultz and Falkenbach, *Merychyus* Leidy, and *Desmatochoerus* (*Paradesmatochoerus*) Schultz and Falkenbach. Comparative Measurements[a] of Skulls and Mandibular Rami

SKULL	*B. r. riograndensis*, new subspecies Holotype F:A.M. 72326	*B. v. riooso-ensis*, new subspecies Holotype F:A.M. 72328	*B. l. mooki*, new subspecies Holotype A.M. 21321,[b] A.M. 21322	*B.* species, Example F:A.M. 72327A	*U. p. nevadaensis*, new subspecies Holotype A.M. 32634	*T. h. leadorensis*, new subspecies Holotype F:A.M. 72334	*M. c. ziaensis*, new subspecies Holotype F:A.M. 72329	*M. arenarum* Cope, tentatively referred Example F:A.M. 72395	*D.* (*P.*) *anthonyi*, new species Holotype F:A.M. 72392
Stage of wear of teeth	(w+)	(m+)	(w$^{++}_{++}$)	(w+)	(m)	(w$^{+}_{+}$)	(w$^{++}_{++}$)	(w+)	(w+)
Length (incl. supraoccipital crest and incisors)	247	—	((300))	—	274	—	—	—	((184))
Basal length (from anterior notch of foramen magnum to posterior base of I¹)	220	—	((260))	—	238	—	—	—	(170)
Width (max.)	138	—	202	—	((180))	—	80	—	(94)
Width of brain case (max.)	69	—	83.5	—	85.5	—	45	(47)	47
Width, interorbital (min.)	(71.5)	—	—	—	85.5	—	43.5	—	(39)
Distance from anterior rim of orbit to anterior base of C/	120.5	—	—	—	108	—	—	79	70
Distance from anterior rim of orbit to supraoccipital crest	135.5	—	—	—	167.5	—	—	—	(118)
Length of nasals	—	—	((44))	—	81.5	—	50	59	—
Width of muzzle at infraorbital foramina	105	—	—	—	80	—	—	—	38
Width across canines	43	—	—	—	50.5	—	((19))	(32)	—
Length, C/–M³ incl.	127.5	141	—	—	132.5	—	64	87	92
Length, P¹–M³ incl.	(113)	125.5	140.5	—	119.5	99	59	78	(82)
Length, P¹–P⁴ incl.	(49)	53	57	—	49	48	27	34	41
Length, M¹–M³ incl.	70	77	85	—	74	52.5	(33)	44.5	(43)
Width of M³ (max.)	24	25	31	—	26	19	12.5	17.5	18
Depth of malar below orbit	35.5	—	—	—	31	—	11.5	(18)	13.5
MANDIBULAR RAMUS									
Length (max., incl. incisors)	—	—	—	250	((228))	—	112.5	—	—
Length, /C to condyle incl.	—	—	—	228	—	—	107.5	—	—
Depth of jaw under coronoid	—	—	—	147.5	—	—	—	—	—
Depth of jaw below anterior edge of M₃	—	—	62	67	49	—	21.5	—	(28)
Length, /C–M₃ incl.	—	—	—	143.5	144.5	—	67.5	—	(92.5)
Length, P₁–M₃ incl.	—	—	—	132	135.5	—	63.5	—	86
Length, P₁–P₄ incl.	—	—	—	52	52	—	25	36	40
Length, M₁–M₃ incl.	—	—	(90.5)	80	84	—	39	—	47.5

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.
[b] A.M. 21321 and 21322 are considered to belong to the same individual.

TABLE 17

Bathygenys DOUGLASS, *Megabathygenys*, NEW GENUS, AND *Parabathygenys*, NEW GENUS. COMPARATIVE MEASUREMENTS[a] OF SKULLS AND MANDIBULAR RAMI

SKULL	*B. alpha* Douglass Referred F:A.M. 72336	*B. a. hedlundae*, new subspecies Holotype F:A.M. 72377	*M. goorisi*, new species Holotype F:A.M. 72385	*P. paralpha*, new species Holotype F:A.M. 72388
Stage of wear of teeth	(w)	(w‡)	(w‡+)	(w)
Length (incl. supraoccipital crest and incisors)	((80))	—	—	—
Basal length (from anterior notch of foramen magnum to posterior base of I^1)	((75))	—	—	—
Width of brain case (max.)	29.5	—	—	—
Width, interorbital (min.)	26	—	—	27
Distance from anterior rim of orbit to anterior base of C/	23	—	26.5	25.5
Distance from anterior rim of orbit to supraoccipital crest	(57.5)	—	—	—
Width of muzzle at infraorbital foramina	21.5	—	—	18.5
Width across canines	—	—	(18)	(13.5)
Length, C/–M^3 incl.	—	—	—	36.5
Length, P^1–M^3 incl.	33.5	—	—	33
Length, P^1–P^4 incl.	17	—	(18.5)	18
Length, M^1–M^3 incl.	17.5	—	—	16.5
Width of M^3 (max.)	6.5	—	—	6.5
Depth of malar below orbit	7.5	—	9.5	5.5
MANDIBULAR RAMUS				
Depth below anterior edge of M_3	—	—	21	—
Length, /C–M_3 incl.	—	—	41.5	—
Length, P_1–M_3 incl.	—	—	39.5	—
Length, P_1–P_4 incl.	—	17	20	—
Length, M_1–M_3 incl.	—	—	19.5	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

In the 1940 and 1941 reports on the oreodonts by the present writers, the range of variation of the skulls was omitted. In order to provide comparisons with later published charts on variation within other subfamilies of oreodonts, charts 11 and 12 (pp. 363–364) present the size range of the Merycochoerinae[1] and the Ticholeptinae.[2] The average and mean measurements of the basal lengths of the skulls and the lengths of P^1–M^3 and P_1–M_3 are recorded.

Tables 16 and 17 contain the measurements of the new material listed in this Appendix.

[1] Schultz and Falkenbach, 1940.

[2] Schultz and Falkenbach, 1941.

MERYCOCHOERINAE, SUBFAMILY 1

Merycochoerinae SCHULTZ AND FALKENBACH, 1940, p. 216.

BRACHYCRUS MATTHEW

Merychochoerus (*Brachycrus*) MATTHEW, 1901, p. 397.

Brachycrus Matthew: SCHULTZ AND FALKENBACH, 1940, p. 218.

DISCUSSION

The skulls and rami of *Brachycrus* are quite distinctive when compared with those of other oreodonts. The large fossae on each side of the face of the skull presumably were used for muscle attachments for the control of a proboscis which probably was similar to that of a modern tapir. Remains of *Brachycrus* are also exceptionally good geologic markers in local areas and are restricted to deposits of late Miocene age, i.e., they are found only in the Sheep Creek (= "Lower Snake Creek" and "Sheep Creek") sediments of Nebraska, or equivalent geologic formations.

The new *Brachycrus* specimens listed in this Appendix throw additional light on the development and geographic distribution of material considered under this interesting genus. It appears to be significant that in all three Rocky Mountain localities, New Mexico (Santa Fe area), Wyoming (Sweetwater River area), and western Montana, the forms developed from small (size of *B. rusticus*) to large (size of *B. sweetwaterensis*), whereas in the Great Plains area (Sheep Creek and Snake Creek localities) the development was from large (size of *B. wilsoni*) to small (size of *B. siouense*).[1] One plausible answer is that the genus had its early development in the Great Plains, where it gradually became smaller. Then the smaller form migrated to the mountain regions, perhaps because of unfavorable climatic conditions. The difference in morphologic character appears to confirm this assumption. The trend to diminish in size may have reversed itself in the higher altitudes, perhaps because of ecological changes, and the oreodonts of this genus gradually began to become larger. At the time of their extinction in the mountain areas, they had attained the size of *B. sweetwaterensis* in the Wyoming region and *B. altiramus* in the Montana area.

When the writers first noted that there was a reversal in size range of the skulls (largest to smallest) in the *Brachycrus* material from the Sheep Creek-Snake Creek area in Nebraska, the geology of the area was not correctly understood. However, further study of the stratigraphy of the beds and a consideration of the balance of the fauna from this area substantiate the sequence of *Brachycrus* from this particular locality in the Great Plains.

The present writers also have considered that the forms in Wyoming had independently evolved contemporaneously with those in the Nebraska region, and that perhaps the two lines should be looked upon as distinct, representing two different subgenera. The problem here, of course, has been to determine an ancestral form common to both lines of development. Some species of a *Merycochoerus*-like oreodont would be an ideal ancestor for *Brachycrus,* but in the upper part of the middle Miocene deposits (= Marsland or equivalent) only large forms are known. It has been difficult to establish an ancestor for the smaller, mountain-dwelling species (*B. rusticus*), especially if one considers the various forms known from the middle Miocene. Hence, it is gratifying to have the additional evidence, which is included in the present paper.

Reed,[2] in a discussion of Miocene insectivores (*Mesocalops scopelotemos*), considered the deposits at Muddy Gap (in the Sweetwater River area) ". . . from the vicinity of the *Brachycrus* quarry (Schultz and Falkenbach)" as a middle Miocene "horizon." The present writers wish to point out that no quarry was found at this locality by the Frick Laboratory field parties when the *Brachycrus* collection was made, and they assume that Reed considered the Sheep Creek deposits, or their equivalents, as middle Miocene age. In the revision of the oreodonts, however, deposits of this age are considered upper Miocene.

ADDITIONAL LISTED SPECIMENS AND DISCUSSIONS[3]

1. **Brachycrus rusticus riograndensis,**[4] new geographic variety

From "Skull Ridge" deposits (approximately equal in age to the lower part of the Sheep Creek Formation), Santa Fe County, New Mexico

Brachycrus, species undetermined: SCHULTZ AND FALKENBACH, 1940, p. 254.

[1] Schultz and Falkenbach, 1940, pp. 232, 242.

[2] 1960, pp. 2, 5.

[3] An unusual occurrence of *Brachycrus* in the Panama Canal Zone has recently been reported by Frank C. Whitmore, Jr., Robert H. Stewart, and Druid Wilson of the United States Geological Survey (letter dated April 2, 1964, to C. Bertrand Schultz from Dr. Frank C. Whitmore, Jr.). (See p. 371 for a preliminary discussion concerning this fascinating occurrence. Previously, oreodonts had not been recorded from south of the United States-Mexico border.)

[4] Named after the Rio Grande Valley of New Mexico in which the holotype was collected.

Description

Skull: Slightly larger than in examples of *B. rusticus*, slightly smaller than in average examples of *B. siouense*; depth of malar moderately shallow, equal to the shallowest examples of *B. siouense*, deeper than in those of *B. rusticus*; smaller and lighter than in examples of *B. vaughani*.

Mandible: (See listing, 1940, p. 254). Same size comparisons as skull.

Dentition: Same size comparisons as skull; definitely lighter than in examples of *B. vaughani*.

Measurements: Table 16 (p. 365).

Illustration: Figure 44.

Discussion

At the time of the publication of the Merycochoerinae in 1940, a skull of *Brachycrus* was not known from the New Mexico area. Several rami were listed under "*Brachycrus*, species undetermined," with the following observation: "The . . . material from New Mexico is represented only by five mandibular rami. The mandibles of the various species of *Brachycrus* are not so readily distinguished as the skulls. Although these specimens from New Mexico compare favorably with *B. siouense*, more material is needed in order definitely to establish the validity of this reference."[1]

Since 1940, two important examples of *Brachycrus* have been added to the collection. One is an almost complete skull, F:A.M. 72326, the holotype of *B. rusticus riograndensis*, from the "middle portion of the lower deposits" (upper Miocene) in the Espanola area of New Mexico. The second is an anterior portion of a skull, F:A.M 72328, the holotype of *B. vaughani rioosoensis*, from the "upper portion of the lower deposits" (upper Miocene) in the same area. Ted Galusha of the Frick Laboratory recorded the geologic occurrences of both specimens in the field.

These geologic data provide evidence that the *Brachycrus* phylum in New Mexico tended to increase in size. (See discussion, p. 428, in reference to retrogression in size of the Nebraska *Brachycrus*.)

One specimen is here recorded:

HOLOTYPE

Skull with I^1–M^3, partial scapula, and partial humerus. (w‡)	F:A.M. 72326	From deposits "in the middle of the upper Miocene," approximately equal in age to the lower part of the Sheep Creek Formation, Skull Ridge, Joe Rak Wash System, Santa Fe County, New Mexico; collected by Ted Galusha and party, 1952 Figure 44 (in part)

2. **Brachycrus vaughani rioosoensis**,[2] new geographic variety

From "Skull Ridge" deposits (approximately equal in age to the upper part of the Sheep Creek Formation), Rio Oso-Abiquiu locality, Rio Arriba County, New Mexico

Description

Skull: (Known from anterior portion only). Larger and more massive than the holotype of *B. rusticus riograndensis*, close to size of examples of *B. vaughani*.

Mandible: (Unknown).

Dentition: Decidedly larger and more massive than in examples of *B. rusticus* and *B. r. riograndensis*; quite similar to examples of *B. vaughani*.

Limbs: (Unknown).

Measurements: Table 16 (p. 365).

Illustration: Figure 46.

Discussion

The holotype of *B. rusticus rioosoensis* comes from an area with a small exposure of deposits here considered as upper Miocene. Ted Galusha, the collector, considers this particular skull as "coming from a zone representing the upper portion of the Upper Miocene." This indicates that the size sequence from New Mexico is from small (*B. rusticus riograndensis* from the middle portion of the upper Miocene deposits) to large (*B. vaughani rioos-*

[1] Schultz and Falkenbach, 1940, p. 254.

[2] Named after the Rio Oso area north of Espanola, Rio Arriba County, New Mexico.

oensis from the upper part of the upper Miocene).

The sequence of small to large size is similar to that found in the Sweetwater River region of Wyoming, and just the reverse of that noted in the Sioux County area of Nebraska.

One specimen is here recorded:

HOLOTYPE

Anterior portion of skull with C/M^3 (P^1 br.). (M+)	F:A.M. 72328	From "Skull Ridge" deposits, "high in the upper Miocene," approximately equal in age to the upper part of the Sheep Creek Formation, Rio Oso-Abiquiu locality, north of Espanola, Rio Arriba County, New Mexico; collected by John C. Blick and Ted Galusha and party, 1942 Figure 46

3. **Brachycrus laticeps mooki**,[1] new subspecies

From upper Miocene deposits (approximately equal in age to the Sheep Creek Formation), "Deep River," Meagher County, Montana

DESCRIPTION

SKULL: Larger than that of *Brachycrus laticeps,* approaching that of *B. sweetwaterensis*; nasals pointed upward, similar to those in *B. laticeps,* more upwardly than in *B. sweetwaterensis*; nasals posteriorly retracted to a point above M^3, more posterior retraction than in latter species.

MANDIBLE: Similar (in available measurements) to that of *B. laticeps.*

DENTITION: Dental series similar to that of *B. laticeps.*

MEASUREMENTS: Table 16 (p. 365).

ILLUSTRATION: Figure 46.

DISCUSSION

The new variety *Brachycrus laticeps mooki* is based on a partial skull and partial mandible. The foregoing characters vary from those of previously known forms, and a complete skull, if known, would add characters that would be of specific value.

The importance of this specimen is in its geographic and geologic occurrence. The remains of *Brachycrus* have been considered to be restricted to upper Miocene deposits.

Koerner[2] used the terms "Fort Logan" and "Deep River" formations, indicating at least two different ages. The oreodonts mentioned by him from this area suggest time equivalents of the Gering and the Harrison formations of the central Great Plains. The *Brachycrus* specimen listed below indicates a third age for deposits in the area. The latter would be approximately equal in age to the Sheep Creek Formation of Nebraska.

Charles C. Mook told us in a conversation several years ago: "The Fort Logan area in Montana is greatly faulted, and blocks, although on the same horizon, may well represent different ages." Falkenbach, who collected in the Fort Logan-White Sulphur Springs area, also found this to be true. There is much need for additional geologic study of the area.

HOLOTYPE

Partial skull with P^1–P^3 rt. and P^4–M^3 br. and left mandibular ramus with P_2–M_2 br. and M_3. (W‡‡)	A.M. 21321 and 21322	From middle Miocene deposits, approximately equal in age to upper part of Sheep Creek Formation, 7 mi. SE. of Fort Logan,[3] Meagher County, Montana; collected by Mook and Williams, 1925 Figure 46

The above skull and mandibular ramus have individual catalogue numbers. However, the writers believe they represent one individual.

[1] Named in honor of Dr. Charles C. Mook, late Associate Curator Emeritus of Fossil Reptiles, the American Museum of Natural History, who was one of the collectors of the holotype.

[2] 1940, p. 57.

[3] This locality is part of the White Sulphur Springs area.

4. **Brachycrus,** species undetermined

From upper Miocene deposits (approximately equal in age to the lower part of the Sheep Creek Formation), Elko County, Nevada

DISCUSSION

The following material is the first evidence of *Brachycrus* remains from the Elko area of Nevada. It is of interest that, in 1929, Barnum Brown of the American Museum of Natural History collected a skull and mandibular ramus of *Ustatochoerus* of Pliocene age (see p. 372) from Antelope Creek, to the west of the Elko area. Recently, J. Regnier and D. W. Lovejoy presented the American Museum of Natural History with a fragmentary skull, A.M. 45280, and a partial mandibular ramus, A.M. 55598, from the Elko area of Nevada. These specimens, although incomplete, are definitely referable to the genus *Brachycrus*.

The fragmentary skull is recognizable as to genus. The mandibular ramus contains P_3–M_3 (br.) and suggests a smaller form than the holotype of *B. laticeps* of Montana, possibly close to examples of *B. buwaldi* from California.

Two specimens are here recorded:

FROM "30 SPEEDOMETER MILES NW. OF ELKO AIRPORT ON HIGHWAY NO. 11," ELKO COUNTY, NEVADA

SKULL | A.M.

Fragmentary skull with I^3–C/ and P^3–M^3 br. and limb fragments . . . . (w+) 45820
The incisors and canine are embedded in plaster, lacking contact with balance of dental series.

MANDIBULAR RAMUS

Partial left ramus with I_1–P_2 rt. and P_3–M_3(br.). Figure 46 . . . . (w‡+) 55598
The only definite measurement on the ramus is the depth below anterior edge of M_3, 60.5 mm. P_1–P_4 (estimated) is 52 mm.

5. **Brachycrus,** species undetermined

From upper Miocene deposits (approximately equal in age to the upper part of the Sheep Creek Formation), Railroad Canyon, near Leadore, Lemhi County, Idaho

DISCUSSION

The Railroad Canyon deposits of Idaho contain upper Miocene deposits (= Sheep Creek age) that extend westward from the Continental Divide about halfway down to the Lemhi Valley. The Lemhi Valley, north of Leadore, includes deposits of both Marsland and Sheep Creek age. (See Schultz and Falkenbach, 1947, p. 186.)

As previously stated, mandibular rami are not sufficiently diagnostic to be the basis of a new species. The importance of this material is that it is a new locality for oreodonts, and the material is definitely referable to the genus *Brachycrus*.

In size, this material is close to examples of *B. vaughani* from Wyoming, but the ramus is deeper below the anterior edge of M_3.

Two specimens are here recorded:

Mandible with /C–M_3. (w+) F:A.M. 72327A From upper Miocene deposits, approximately equal in age to upper part of Sheep Creek Formation, Railroad Canyon, near Tunnel Draw, Lemhi County, Idaho; collected by Charles H. and Charles F. Falkenbach, 1950
Figure 46

REFERRED, FOUND ASSOCIATED WITH THE "EXAMPLE" IN THE FIELD

MANDIBLE, IMMATURE | F:A.M.

Partial mandible with I_1–dP_1–M_3(germ) . . . . (I) 72327B

6. **Brachycrus buwaldi** (Merriam)

From upper Miocene deposits approximately equal to the upper part of the Sheep Creek Formation (= "Lower Snake Creek") in age, from the Barstow area, San Bernardino County, California

Brachycrus buwaldi (Merriam): SCHULTZ AND FALKENBACH, 1940, p. 223.

DISCUSSION

In 1949 Schultz and Falkenbach[1] published a geologic distribution chart that inadvertently showed *Brachycrus buwaldi* and *B. buwaldi barstowensis* occurrences approximately equivalent to the "Sheep Creek" of the Great Plains. They[2] had previously correctly reported that "*Brachycrus* remains in the Barstow area are recorded only from the Green Hills horizon or Second Division which underlies the later deposits . . . of the First Division." This "Green Hills horizon or Second Division" is approximately equal in age to the "Lower Snake Creek" (upper part of the Sheep Creek or, as the present writers use the term, of the Great Plains).

Lewis (*in* Byers, 1960, p. 33) showed that *Brachycrus buwaldi* occurs 500 feet higher stratigraphically than *Merychippus tehachapiensis* in the Barstow Formation of the Alvord Mountain area; *M. tehachapiensis* is of "Sheep Creek" age comparable to that of *M. primus,* so *B. buwaldi* must be appreciably younger than indicated on the geologic chart mentioned above. Also, *Merychyus* (*Metoreodon*) *relictus fletcheri* Schultz and Falkenbach[3] was attributed to the "Red or Third Division" of the Miocene deposits north of Barstow. This was mistakenly shown above the Second Division on the 1949 geologic distribution chart, but should have been shown in descending sequence below the Second Division as approximately equal in age to the "Sheep Creek" Formation of the Great Plains.

UNUSUAL OCCURRENCE OF *Brachycrus* IN PANAMA CANAL ZONE

Since the present manuscript was completed for press, and unusual occurrence of *Brachycrus* has been recorded from the Panama Canal Zone by Frank C. Whitmore, Jr., and Robert H. Stewart[4] of the United States Geological Survey. Frank C. Whitmore, Jr., showed the specimens from the Panama Canal Zone to C. Bertrand Schultz in November, 1963, and at that time Schultz agreed that the specimens definitely could be identified as *Brachycrus,* and that they closely resembled material from the Great Plains region of the United States. On April 2, 1964, Whitmore wrote Schultz the following in a letter, and gave permission to quote the information, which also is included in the 1965 report of Whitmore and Stewart. "The crushed skull of an immature merycochoerine merycoidodont, tentatively assigned to the genus *Brachycrus,* was found by Robert H. Stewart in the Cucaracha Formation in the Panama Canal Zone. The locality is at Station 1998/00, 600 feet west of the center line of the Panama Canal. *Diceratherium* sp. and an unnamed protoceratid, as well as crocodiles and turtles, were also found."

DISCUSSION

The Panama Canal Zone specimen is the first recorded occurrence of oreodonts from south of the United States-Mexico border. Oreodonts are known from Texas, New Mexico, and California, all states that border on Mexico, but no specimens had been reported from the southern part of the North American continent.

The finding of *Brachycrus* in the Panama Canal Zone area may help support the contention of the present writers that the genus does not represent a typical plains or grassland type of animal. The oreodonts of the *Merycochoerus-Brachycrus* phylogenetic line appear to have evolved gradually from typical plains forms to river valley-forest living animals.

TICHOLEPTINAE, SUBFAMILY 2

Ticholeptinae SCHULTZ AND FALKENBACH, 1941, p. 1.

USTATOCHOERUS SCHULTZ AND FALKENBACH

Ustatochoerus SCHULTZ AND FALKENBACH, 1941, p. 10.

DISCUSSION

The genus *Ustatochoerus* represents the latest (geologically) of the oreodonts. The time range is from early Pliocene (lower part of Valentine Formation) to middle Pliocene (upper part of middle Ash Hollow Formation).

[1] Chart 1, p. 80.
[2] Schultz and Falkenbach, p. 224.
[3] Schultz and Falkenbach, 1947, p. 245.
[4] 1965, p. 180.

The additional material here listed adds four new localities, from Nevada, Nebraska, and Texas.

1. **Ustatochoerus profectus nevadaensis,** new geographic subspecies

From Pliocene deposits (approximately equal in age to the lower Ash Hollow Formation), Elko County, Nevada

Description

SKULL: Within expected size range of examples of *U. profectus*; close to size of that of *U. profectus studeri* from Texas.

MANDIBLE: Same size comparison as skull, except that ramus is deeper below anterior border of M_3.

DENTITION: Complicated premolars characteristic of genus; same size comparisons as skull.

LIMBS: (Unknown).

MEASUREMENTS: Table 16 (p. 365).

ILLUSTRATION: Figure 45.

Discussion

The holotype of this new geographic species is important because it came from Pliocene deposits northeast of Battle Mountain, Nevada. The specimen was collected by Barnum Brown in 1929 but not brought to the attention of the present writers until after their publication on the Ticholeptinae. The specimen created interest in the locality, and Falkenbach took a party into the area in 1942 and 1956. The visits were profitable but yielded no additional oreodont material. It may be assumed that *Ustatochoerus* remains are rare in the area.

Actually the holotype does not vary from the *U. profectus* material from Nebraska. Perhaps, if and when additional specimens are available, there may be a size trend that would separate the *Ustatochoerus* examples of Nevada from those of Nebraska.

One specimen is here recorded:

HOLOTYPE

Partial skull with I^1–M^3 and partial left ramus with /C–M_3 (P_2 rt.). (M)	A.M. 32634	From Pliocene deposits approximately equal in age to the lower part of Ash Hollow Formation, Antelope Valley, 60 mi. NE. of Battle Mountain, Elko County, Nevada; collected by Barnum Brown, 1929 Figure 45

2. **Ustatochoerus major** (Leidy), referred

From the middle part of the Ash Hollow Formation, Morrill County, Nebraska

Ustatochoerus major (Leidy): SCHULTZ AND FALKENBACH, 1941, p. 16.

Discussion

The following specimens are referable to *U. major* and occur in deposits approximately equal in age to that of the Xmas Quarry level (middle part of Ash Hollow Formation).

The U.N.S.M. specimens were collected by E. L. Blue, Mylan Stout, Lloyd Tanner, Marian and Bertrand Schultz, and associates, 1941.

Five specimens are here recorded:

REFERRED FROM UNIVERSITY OF NEBRASKA STATE MUSEUM COLL. LOC., BW, LOC. B, Q2, NORTH OF BROADWATER, MORRILL COUNTY, NEBRASKA

5 MANDIBULAR RAMI

		U.N.S.M.
3 partial mandibles with		
I_1–I_2 rt. and I_3–M_2 (I_3 and M_1 br.)	(w‡)	28614
I_1–P_2 alv. and P_3–M_3	(w+)	28610
I_3–dP_2–M_3(erupt.)	(I)	28612
2 partial left rami with		
M_3	(w‡)	28615
M_3 br.	(w‡)	28616

The above specimen may be from the same individual as the partial mandible, U.N.S.M. 28614.

3. **Ustatochoerus,** species undetermined

From the Valentine Formation, Franklin County, Nebraska

DISCUSSION

The following three specimens here recorded add a new locality to the geographic distribution of the oreodonts and represent an eastern extension in the central Great Plains oreodont fauna. These examples of *Ustatochoerus* were collected by Allen Graffham, C. Bertrand Schultz, and associates, 1948.

REFERRED FROM UNIVERSITY OF NEBRASKA STATE MUSEUM COLL. LOC. FR-20, SOUTHEAST OF NAPONEE, FRANKLIN COUNTY, NEBRASKA

3 MANDIBULAR RAMI		U.N.S.M.
Partial right ramus with P_3–M_3	(w+)	28625
Fragment of right ramus with M_3(br.)	(w‡)	28626
Partial left ramus with I_1–/C alv. and P_1(rt.)–P_3(br.)	(w‡)	28627

4. **Ustatochoerus,** species undetermined

From Pliocene deposits (approximately equal in age to the Valentine Formation), Bee County, Texas

Ustatochoerus: QUINN, 1955, p. 72.

DISCUSSION

James Quinn presented the writers with two casts of *Ustatochoerus,* one a maxilla and the second a partial mandibular ramus. The original specimens are from southern Texas and are considered to be representative of the Lapara Creek fauna. Both examples of *Ustatochoerus* are the approximate size of examples of *U. medius* from the Valentine of Nebraska and also have other characters similar to those of this species, but the present writers do not consider the two examples complete enough for specific identification.

Quinn[1] discussed the faunas and their geologic sequence, which differs from the present writers' conception (see chart 13, p. 411) of the correlation with the Great Plains sequence. Quinn spent considerable time and effort on his studies of the faunas, but his conclusions do not agree with the evidence gained from our study of the oreodonts. We realize that part of the difference of opinion may be due to the fact that there is no general agreement on the geologic age of the Valentine Formation and other deposits approximately equal in age. Quinn (p. 76) acknowledged this Miocene-Pliocene boundary question in the following discussion: "There is a question as to the advisability of drawing the Miocene-Pliocene boundary between the deposits containing the Burge and Lapara Creek faunas. If the longheld thesis is correct that the 'Pliocene' horses suddenly replaced *Merychippus* in the central and western regions and if this event is taken as the beginning of Pliocene time, as advocated by McGrew and Meade (1938) and others, there is ample justification for assigning the Lapara Creek to the Miocene since the Lapara Creek must have furnished the stock that replaced *Merychippus* in the north and west at that time."

The present writers acknowledge that the horses or any other mammalian group may also provide "index fossils" or geologic faunal-zone indicators as excellent as the oreodonts. However, a complete revision of any group of mammals, based on stratigraphic as well as morphologic evidence, must be made before the phylogenetic history can be determined. Evidence gained from similar revisions should provide additional important facts concerning faunal breaks and rates of development in different phylogenetic lines.

Under additions to *Ticholeptus* (p. 375), the occurrence of *T. rileyi* is discussed. A discussion of its geologic occurrence, however, seems pertinent here, as it is apparently a part of the "Lapara-Cold Spring" faunal problem. Quinn[2] reported, "The Cold Spring fauna is distinguished by the first appearance of proboscideans, *Alticamelus, Procamelus* and *Teleoceras.*" He (p. 72) also included *Ticholeptus rileyi* as part of the Cold Spring fauna. The present writers consider that his "fauna" includes faunal elements ranging in age from upper Miocene to lower Pliocene. Also it is here considered that the lower portion of the deposits of the Coldspring area are of upper

[1] 1955, pp. 67–72, tables 25–27.

[2] 1955, p. 71.

Miocene age (equal to the "Lower Snake Creek" of Nebraska) and that the upper portion of the same deposits are Pliocene (probably equal in age to the Valentine of Nebraska).

The following statements by Quinn[1] are confusing to those who have worked with the literature and the stratigraphically documented collections of the Frick Laboratory and the University of Nebraska State Museum from the Valentine-Ainsworth area: "The exact stratigraphic position of the [Matthew's] Ainsworth material is not known. It is lower than that of the Lower Ash Hollow fauna (of the Valentine Formation) and may be equivalent to the Burge fauna." The geological section (chart 13, p. 411, and elsewhere) used by Schultz and Falkenbach throughout the oreodont revisions shows the relationship of the Valentine Formation (including Burge Member) to the Ash Hollow Formation. This generalized section is based on measured sections and is widely accepted by the geologists who have been working in the area. The oreodont faunas of the lower Ash Hollow and the Valentine (including the Burge local fauna) are distinct from each other, as are those of the "Lower Snake Creek" and Valentine.

Wilson[2] came to essentially the same conclusions as did Quinn in reference to the ages of the deposits of the Coldspring area and the Lapara Formation. Much depends on the completeness of specimens used for the basis for these conclusions.

James Quinn and Charles H. Falkenbach, both of whom collected in the Coldspring area, discussed the age of the Coldspring deposits as possibly including two geologic ages, upper Miocene and Pliocene. It was Falkenbach's understanding that the material available to Quinn for study was collected primarily by W.P.A. field parties and by Claude Riley. Just how much data were available with the Coldspring material is not known. Claude Riley appeared to remember the localities of the various specimens collected by him, especially the stratigraphic levels of the mastodonts. He indicated that the mastodonts came from the "upper zone."

It should be noted that the name of the town, Coldspring, Texas, has been spelled Coldspring, Cold Spring, or Cold Springs in various geologic and paleontologic publications. The United States Official Postal Guide (July, 1953, p. 503) lists the name as one word, Coldspring. The present writers have used Coldspring as a locality and town name in this report, but also have used the name Cold Spring when referring to the faunal zone, geologic horizon, or deposits.[3] Dumble[4] spelled the name "Cold Springs" when he originally named the geologic horizon.

A comparison of Quinn's and Wilson's geologic conclusion with the conclusions of the present writers, based on the Central Great Plains section, is given in table 18.

Two examples of *Ustatochoerus*, species undetermined, are here recorded:

EXAMPLES FROM BEE COUNTY, TEXAS

Partial right maxilla with C/(br.)–M^3(br.). (w)	B.E.G., U.T. 31081–685	From near Berclair
Partial right ramus with P_4(br.)–M_2. (w‡)	B.E.G., U.T. 31170–25	From near Normana

TICHOLEPTUS Cope

Ticholeptus Cope, 1878b, p. 129. Schultz and Falkenbach, 1941, p. 72.

Discussion

The genus *Ticholeptus* evidently represents the late Miocene ancestral line that gave rise to the *Ustatochoerus* phylum. The genus is restricted to the Sheep Creek Formation or deposits equal in age.

1. **Ticholeptus rileyi** Schultz and Falkenbach

From upper Miocene deposits (approximately equal in age to the upper part of the Sheep Creek Formation), San Jacinto County, Texas

Ticholeptus rileyi Schultz and Falkenbach, 1941, p. 83. Quinn, 1955, pp. 70–76.

[1] 1955, p. 75.
[2] 1959a.
[3] See Wilmarth, 1938, p. 485.
[4] 1915, p. 468.

TABLE 18

COMPARISON OF GEOLOGIC CONCLUSIONS OF QUINN (1955) AND WILSON (1959A) WITH THOSE OF SCHULTZ AND FALKENBACH, BASED ON THE CENTRAL GREAT PLAINS SECTION

Epoch	Groups	Formations	Nebraska	Texas (Schultz and Falkenbach)	Texas Faunas (Quinn)
Pliocene	Ogallala	Middle Ash Hollow	Kat Quarry or equivalent		
		Lower Ash Hollow	Cap Rock or equivalent		
		Valentine	Burge Quarry, Devil's Gulch Horse Quarry or Equivalent	[Lapara] Cold Spring (upper deposits)	
Miocene	Hemingford	Sheep Creek	"Lower Snake Creek"	Cold Spring (lower deposits)	Lapara[b] Creek
			"Sheep Creek"		
		Marsland	Marsland area		Cold Spring
	Arikaree[a] (in part)	Harrison	Harrison area		Garvin Gully[c]

[a] The Arikaree Group also includes two lower formations: the Gering and Monroe Creek (see chart 13, p. 411).

[b] Quinn considered the Lapara as upper Miocene (Barstovian), Cold Spring as middle Miocene, and Garvin Gully as lower Miocene. The present authors consider the Barstovian as lower Pliocene (=Valentine Formation) in age.

[c] See p. 378.

DISCUSSION

The holotype of *T. rileyi* was collected by Claude Riley from the lower portion of the Miocene-Pliocene deposits near Coldspring, Texas. The specimen compares readily with examples of *Ticholeptus* from the "Lower Snake Creek" deposits (= upper portion of Sheep Creek Formation) of Nebraska (upper Miocene).

Quinn considered the Cold Spring fauna as Hemingfordian (middle Miocene), just below the Lapara Creek. A comparison of the geologic sequence in Nebraska with that of Quinn's sequence in Texas is illustrated in table 18.

2. **Ticholeptus hypsodus leadorensis,**[1] new subspecies

From upper Miocene deposits (approximately equal in age to upper part of Sheep Creek Formation), Railroad Canyon, near Leadore, Lemhi County, Idaho

DESCRIPTION

SKULL: Slightly larger than in examples of *Ticholeptus hypsodus* from Nebraska.

MANDIBLE: (Unknown).

DENTITION: Series longer, especially premo-

[1] Named after the town of Leadore, which is at the west end of Railroad Canyon, Idaho.

lars, and more robust than in that of *T. hypsodus*.

LIMBS: (Unknown).

MEASUREMENTS: Table 16 (p. 365).

ILLUSTRATION: Figure 44.

DISCUSSION

The holotype of *Ticholeptus hypsodus leadorensis* is an incomplete and crushed specimen. The specimen is of interest primarily because of its geologic (= approximately to upper part of Sheep Creek Formation) and geographic (Nevada) occurrences. Remains of *Brachycrus* also are now known from the same deposits (see p. 370). The association of *Brachycrus* and *Ticholeptus* is common in Upper Sheep Creek or equivalent deposits in the Great Plains.

One specimen is here recorded:

HOLOTYPE

Partial skull with C/–M^3. (w‡$^+$)	F:A.M. 72334	From upper Miocene deposits approximately equal in age to the upper part of the Sheep Creek Formation, 1 mi. W. of Continental Divide, 20′ below top of exposure in Tunnel Draw, Railroad Canyon, Lemhi County, Idaho; collected by Charles H. and Charles F. Falkenbach, 1950 Figure 44

3. **Ticholeptus,** species undetermined (Merriam)

From upper Miocene deposits (approximately equal in age to the upper part of the Sheep Creek Formation), Virgin Valley, Humboldt County, Nevada

Ticholeptus, species undetermined (Merriam)
Thorpe: SCHULTZ AND FALKENBACH, 1941, p. 86.

DISCUSSION

Schultz and Falkenbach (1941) listed a lower and upper molar from Merriam's collection under "*T.*, species undetermined," and stated: "The two specimens are inadequate for definite generic identification. The teeth are slightly larger than examples of *Ticholeptus* and approach those of *Ustatochoerus? schrammi* in size." An additional specimen, a partial maxilla, F:A.M. 72335, is about the size of *T. hypsodus*.

One specimen is here recorded:

Partial left maxilla with P^4–M^2. (w)	F:A.M. 72335	From ½ mi. W. of junction of Virgin Valley and Cedarville roads, Humboldt County, Nevada; collected by Paul Geygan and Charles H. Falkenbach, 1956 Figure 44

4. **Ticholeptus,** species undetermined

From upper Miocene deposits (approximately equal in age to the upper part of Sheep Creek Formation), Elko County, Nevada

DISCUSSION

A fragmentary, immature, partial mandibular ramus, A.M. 45821, is here referred to the genus *Ticholeptus*. The importance of this specimen is that it evidently occurred in the same deposits as the *Brachycrus* remains (see p. 370, this publication).

One specimen is here recorded:

Partial left ramus with P_2–dP_4–M_2. (I)	A.M. 45821	From upper Miocene deposits, approximately equal in age to upper part of Sheep Creek Formation, 30 mi. NW. of Elko airport, Elko County, Nevada; collected by J. Regnier and D. W. Lovejoy, presented to A.M.N.H., 1957

MERYCHYINAE, Subfamily 3

Merychyinae Schultz and Falkenbach, 1947, p. 168.

MERYCHYUS Leidy

Merychyus Leidy: Schultz and Falkenbach, 1947, p. 171.

1. **Merychyus crabilli ziaensis,**[1] new subspecies

From lower Miocene deposits (approximately equal in age to the Harrison Formation), Sandoval County, New Mexico

Description

Skull: Smaller than that of examples of *M. crabilli*; slightly longer nasal than in that species; more depressed than in *M. crabilli.*[2]

Mandible: Smaller and lighter than in examples of *M. crabilli.*

Dentition: (Known only from a very old individual). Series smaller and lighter than in those of *M. crabilli.* (It is of interest that the holotype lacks M^1 on the left side and M^1–M^2 on the right. These were lost during life. The absence of these teeth is reflected in the crown view, fig. 44.)

Limbs: Decidedly lighter than those of *M. crabilli.*

Measurements: Table 16 (p. 365).

Illustration: Figure 44.

Discussion

The holotype of *Merychyus crabilli ziaensis* is similar to that of *M. crabilli* except for smaller size of the skull, mandible, and limb elements. The loss, in life, of the left M^1 and right M^1–M^2 caused the posterior teeth to migrate slightly forward. The heels of both left and right M^3 are exceptionally large.

This is the first evidence from New Mexico of oreodonts in the lower Miocene (approximately equal in age to the Harrison Formation of the central Great Plains). The oreodont fauna from New Mexico now includes *Merychyus crabilli ziaensis* from a Harrison equivalent, *M.* (*Metoreodon*) species and *Brachycrus* species from an equivalent of Sheep Creek age, and *Ustatochoerus* remains from the Valentine to the upper part of the middle Ash Hollow, or perhaps the lower part of the upper Ash Hollow. The oreodonts appear to have survived longer in New Mexico than in any other region in North America.

One specimen is here recorded:

HOLOTYPE

Partial skull with I^1–M^3 (lacking M^1), mandible with I_1–M_3, partial humerus, partial ulna and radius, partial tibia, partial metacarpal, and fragments. (w‡‡)	F:A.M. 72329	From lower Miocene deposits, "pinkish band of sediments in gray sand," approximately equal in age to the Harrison, N. side of Canyada Pilares, Sandoval County, New Mexico; collected by Ted Galusha and party, 1951 Figure 44

2. **Merychyus arenarum** Cope, tentatively referred

From deposits approximately equal in age to the lower Marsland Formation, Carter County, Montana

Merychyus arenarum Cope: Schultz and Falkenbach, 1947, p. 175, figs. 1, 3, 13–17.

Discussion

The dentition and limb elements, in appearance and measurements, are very similar to examples of *M. arenarum* and *M. a. idahoensis.*[3] Unfortunately the tentatively referred material does not include the posterior portion of a skull.

Both the upper and lower canines of the Montana specimens are short and are similar to those of *M. arenarum* (from Wyoming) and examples of *M. a. idahoensis* (from Idaho). In the former, both large and small canines are known. The limb proportions are considerably different from examples of the subgenus *M.* (*Metoreodon*).

The Chalk Buttes area is north and slightly

[1] Named after the Zia Pueblo, which is in the same region in which the holotype was collected.

[2] Possibly owing partly to the vertical crushing of the holotype of the new subspecies.

[3] Schultz and Falkenbach, 1947, pp. 175, 186.

west of the Wyoming lower Marsland deposits from which many examples of *M. arenarum* have been collected. Since the posterior portion of the skull is lacking, the writers have concluded that no definite specific classification is possible at this time.

The following material was collected by Morris F. Skinner and party in 1954. Its primary importance is the recording of a new location for the geographic distribution of the oreodonts. (See table 16.)

Two specimens are here recorded:

From Lone Butte, West Side of Chalk Buttes, Carter County, Montana:

2 SKULLS, MANDIBLES, AND SKELETAL ELEMENTS

Anterior portion of skull with I^1–M^3, partial mandible with I_1–M_3(br.), partial scapula, 2 partial humeri, 2 radii, 2 ulnae, 2 partial manus, 2 partial femora, 2 partial tibiae, 2 astragali, 2 calcanea, 2 partial pedes, and a partial pelvis	(W+)	F:A.M. 72395
Anterior portion of skull with I^1–M^3, partial mandible with P_1–P_4, and partial humerus	(M+)	72396

3. **Merychyus,** species undetermined

From near Independence, Washington County, Texas

Merychyus Quinn, 1955, p. 73.

Discussion

Quinn[1] included the genus *Merychyus* in the Garvin Gully fauna. As he stated, "The [Garvin Gully] fauna has been collected from various sites between Huntsville, Walker County and La Grange, Fayette County." Quinn presented the writers with a cast of a mandibular ramus (B.E.G. No. 40105-5) lacking teeth. This cast may be of a *Merychyus* or *M.* (*Metoreodon*) or even an immature *Ticholeptus rileyi.*

Quinn did not cite this specimen by number, and it is questionable which specimen he concluded to be that of *Merychyus* occurring in the Garvin Gully fauna. The localities included by Quinn for the Garvin Gully local fauna appear to be all of the same approximate age, but it is difficult to determine what particular specimens are involved.

This *Merychyus* ramus (mentioned above) has I_3–P_3 alveoli with questionable P_4 or dP_4 broken. If the ramus is of a mature individual, it is the size of that of *Merychyus crabilli* from the Harrison (lower Miocene) of the Great Plains. If it is of an immature animal, it could be equal to that of a species of *M.* (*Metoreodon*) or even *Ticholeptus rileyi,* both of which are derived from Sheep Creek sediments (upper Miocene) or from deposits of equivalent age.

It is apparent that Quinn's interest and conclusions were based primarily on the equids from the various localities. The evidence of oreodont occurrences reported by Quinn seems far from conclusive. (See pp. 373 and 374 for further discussion of oreodont occurrences in Texas reported by Quinn.)

One specimen is recorded:

MANDIBULAR RAMUS

Cast of partial left ramus with I_3–P_3 alveoli (with dP_4(br.) or P_4 br.)	B.E.G., U.T. 40105–5	From Independence, Washington County, Texas

4. **Merychyus,** species undetermined

From lower or middle Miocene deposits (approximately equal in age to the Harrison or lower Marsland), Beaverhead County, Montana

Discussion

Oreodont remains from this Sage Creek area are known from a partial ramus and skeletal fragments. These represent a form close in size to examples of *Merychyus crabilli* from the Harrison of the Great Plains.

The material here listed is not complete enough for specific identification but does relate the genus *Merychyus* to this area. It is possible that the fragments represent a form similar to *M. minimus* from the lower Marsland of the Great Plains.

[1] 1955, p. 72, table 24, p. 73.

One specimen is here listed:

Partial right mandibular ramus with dP_4(br.)–M_1, partial radius and ulna, 2 partial metapodials, and second phalanx. (I)	F:A.M. 72391	From lower or middle Miocene deposits, equal in age to Harrison or lower Marsland, 4–5 mi. E. and S. of Cook Ranch type section, Beaverhead County, Montana; collected by Dan Krochak and Charles H. Falkenbach, 1954

MERYCHYUS (METOREODON)
(MATTHEW AND COOK)

Merychyus (*Metoreodon*) (Matthew and Cook): SCHULTZ AND FALKENBACH, 1947, p. 232.

1. **Merychyus (Metoreodon),** species undetermined, Schultz and Falkenbach

From upper Miocene deposits, lower part of the "Santa Fe Beds," (approximately equal in age to the Sheep Creek Formation), east of Espanola, Santa Fe County, New Mexico

Merychyus (*Metoreodon*), species undetermined: SCHULTZ AND FALKENBACH, 1947, p. 245.

DISCUSSION

The specimens of the subgenus available from New Mexico in 1947 consisted of a partial maxilla and limb elements of an aged individual and limb elements of a second individual. The new material includes a well-preserved mandible from "Skull Ridge," Santa Fe County, New Mexico; and also a partial maxilla and mandibular ramus of a third individual, all from a new locality for the oreodonts, namely, "Kiva Quarry," Sandoval County, New Mexico.

The new material adds very little to the identifiable characters of the form. The mandible, F:A.M. 72333 (fig. 47) demonstrates the likeness to *M.* (*M.*) *relictus* from Nebraska. This is the same conclusion as was drawn by the writers in 1947.

Four specimens are here recorded:

Mandible with I_1–I_3 alv. and /C–M_3. (w‡⁺)	F:A.M. 72333	From upper Miocene deposits, "just above channel on crest, South Skull Ridge," Santa Fe County, New Mexico; collected by Ted Galusha and party, 1948 Figure 47

FROM "KIVA QUARRY," ABOUT TWO MILES SOUTHWEST OF ZIA PUEBLO, SANDOVAL COUNTY, NEW MEXICO (COLLECTED BY TED GALUSHA AND PARTY, 1950)

MAXILLA AND MANDIBULAR RAMUS		
Partial left maxilla with P^3–P^4 br. and M^1–M^2 and left ramus with I_1–M_3 (/C–M_1 br.)	(M+)	F:A.M. 72330
MANDIBULAR RAMI		
Partial mandible with I_1–dP_3–M_2(germ)	(I)	72331
Partial right ramus with M_2–M_3	(W)	72332

2. **Merychyus (Metoreodon),** species undetermined

From upper Miocene deposits (approximately equal in age to the upper part of the Sheep Creek Formation), Railroad Canyon, near Leadore, Lemhi Valley, Idaho

DISCUSSION

The available material is not sufficient for definite specific identification. The illustrated example (fig. 47) is a partial skull and partial mandible, and the dentition is abnormal. M^3 is elongated (anteroposteriorly) and has three well-developed lobes in place of the normal two lobes and a heel. The skull measurements are within the range of those of known *M.* (*Metoreodon*) examples. The dentition, however, is longer anteroposteriorly.

The mandibular ramus of the same figured specimen is deeper below M_3 than in other examples of the subgenus. The inferior dental series is comparable to the superior series and is longer than in other examples of the subgenus. It is possible that the longer measurements for the superior and inferior dental series are due to the abnormal length and shape of M^3. The present writers concluded that it would be best not to use an abnormal specimen as a holotype for a new species.

The primary importance of the occurrence of an example of *Merychyus* (*Metoreodon*) in the upper Miocene deposits of Lemhi Valley in Idaho is that remains of *Brachycrus* (see p. 370) were found in the same deposits. This association would be expected, since both genera are recorded from the same deposits in other localities.

Two specimens are here recorded:

Partial skull with I^1–P^1 rt. and P^2–M^3, mandible with I_1–M_3, partial ulna, and fragments. (w)	F:A.M. 72389	From upper Miocene deposits, approximately equal in age to the upper part of the Sheep Creek Formation, Railroad Canyon, W. of Tunnel Draw, Lemhi County, Idaho; collected by Charles H. and Charles F. Falkenbach, 1950 Figure 47

The above specimen contains abnormal M^3's, each of which has three distinct lobes.

REFERRED FROM SAME AREA

MAXILLA, IMMATURE		F:A.M.
Partial left maxilla with P^1–dP^3–M^1	(I)	72390

3. Merychyus (Metoreodon) relictus taylori
Schultz and Falkenbach

From upper Miocene deposits [approximately equal to the lower part of the Sheep Creek Formation (= "Sheep Creek") in age], from the Barstow area, San Bernardino County, California

Merychyus (*Metoreodon*) *relictus taylori* SCHULTZ AND FALKENBACH, 1947, p. 241.

DISCUSSION

In 1949 Schultz and Falkenbach[1] published a geologic chart that showed *Merychyus* (*Metoreodon*) *relictus fletcheri* as approximately equivalent in age to the "Lower Snake Creek" of the Great Plains. They[2] had previously reported in the original description of the subspecies that the unique specimen (the holotype) came from the "Red or Third Division" of the Barstow Formation.

G. Edward Lewis (written communications of 1955 to 1960, and reports in press) has pointed out to the present writers that *Merychyus* cf. *M. relictus* also occurs with *Brachycrus buwaldi* in the "Green Hills" or "Second Division" and with *Merychippus tehachapiensis* in the lowest faunal assemblage ("Red Division" of the reports on the Frick collections) of the Barstow Formation. He thoughtfully suggested (written communication) that the present writers may have inadvertently misplaced *M.* (*M.*) *relictus fletcheri* in the 1949 geologic distribution chart and that its stratigraphic position in the "Red or Third Division" underlies (rather than overlies) the "Second Division" in normal numerical sequence and is approximately equivalent in age to the "Sheep Creek" Formation of the Great Plains.

[1] Chart 1, p. 80.
[2] 1947, p. 245.

DESMATOCHOERINAE, SUBFAMILY 6

Desmatochoerinae SCHULTZ AND FALKENBACH, 1954, pp. 107, 193.

DESMATOCHOERUS THORPE

Promerycochoerus (*Desmatochoerus*) THORPE, 1921a, p. 241.

1. Desmatochoerus curvidens gregoryi
(Loomis), referred

From lower Miocene deposits, Harrison Formation, Cherry County, Nebraska

DISCUSSION

The importance of the following listed specimen is that its geographic occurrence marks a new locality for deposits of Harrison age.

One specimen is here recorded:

Partial skull with P^3–M^3. (w+)	F:A.M. 72394	From Harrison deposits, bluff on east side of Niobrara River, 7 mi. S. and 1 mi. W. of Merriman, Cherry County, Nebraska; collected by Morris Skinner and associates, 1952

DESMATOCHOERUS (PARADESMATOCHOERUS)
SCHULTZ AND FALKENBACH

Desmatochoerus (*Paradesmatochoerus*) SCHULTZ AND FALKENBACH, 1954, p. 193.

2. ?Desmatochoerus (Paradesmatochoerus) anthonyi,[1] new species

From Lower Miocene deposits, upper part of Gering Formation, Goshen County, Wyoming

DESCRIPTION

SKULL: Comparatively long and narrow, smaller than in previously known examples of *Desmatochoerus* or *D.* (*Paradesmatochoerus*); sagittal crest prominent; orbit rounded; large and deep lacrimal fossa; facial vacuity present or absent; nasal-maxilla in area above midline of P^1; auditory bulla inflated, more rounded than narrow transverse examples of subgenus; postglenoid more peg-shaped than in usual examples of subgenus.

MANDIBLE: Light; postsymphysis below P_3; less depth to ramus below M_3 than in *D.* (*P.*) *sanfordi.* [Other characters similar to those of examples of *D.* (*P.*) *sanfordi.*]

DENTITION: Series smaller (anteroposteriorly) than in examples of *D.* (*P.*) *sanfordi*; P^1–P^3 each with moderately strong anterior intermediate crest; P_2–P_3 each with moderately prominent posterior intermediate crest; C/ and P_1 moderately large.

LIMBS: (Unknown.)

MEASUREMENTS: Table 16 (p. 365).

ILLUSTRATION: Figure 47.

DISCUSSION

The holotype of this species is an excellently preserved skull and ramus. It occurred in deposits that are approximately equal in age to those yielding examples of *Desmatochoerus* (*Paradesmatochoerus*) *sanfordi* (Gering Formation). The holotype of *D.* (*P.*) *sanfordi* is not a well-preserved specimen, and it represents a very old individual.

A referred specimen, F:A.M. 72393, consisting of a poorly preserved skull and right mandibular ramus, is also here questionably referred to *?D.* (*P.*) *anthonyi.* The general characters of the holotype and referred specimen are approximately the same, and the dentitions are of similar size. The posterior portion of the referred skull, however, is shorter than that of the holotype.

Morris F. Skinner, the collector of the questionably referred specimen, considers its geologic occurrence as "middle part of Whitney Formation." The present writers have spent considerable time in this area, and Falkenbach, who made a large collection in this area, believed that this particular occurrence was in the Gering.

In this area there are both Miocene and Oligocene deposits. However, there are ash zones in the Gering that may be mistaken for those of the Whitney. The referred specimen is not typical of any known form from the Oligocene, but its affinities are close to the Miocene Desmatochoerinae.

Two specimens are here recorded:

HOLOTYPE

Skull with I^1–M^3 and left mandibular ramus with I_1–M_3. (w+)	F:A.M. 72392	From Gering Formation,[2] 3½ mi. E. of Tremain, Horse Creek area, Goshen County, Wyoming; collected by Nelson J. Vaughan, Gene Roll, and Charles H. Falkenbach, 1938 Figure 47

[1] Named in honor of Dr. Harold E. Anthony, long-time Chairman of the Department of Mammalogy of the American Museum of Natural History, Curator in the Frick Laboratory (1958–1966), and now Curator Emeritus.
[2] The Gering in this area represents the upper part of the Gering.

QUESTIONABLY REFERRED FROM 66 MOUNTAIN, GOSHEN COUNTY, WYOMING (COLLECTED BY MORRIS SKINNER AND PARTY, 1957)

SKULL AND MANDIBULAR RAMUS

Partial skull with C/–M^3 (P^4–M^2 br.) and partial right ramus with /C(rt.)–M_3 (P_4 rt.) Figure 47 . . . . (w‡+) F:A.M. 72393

Morris F. Skinner, who collected this specimen, recorded it as from the "middle part of the Whitney Formation." It is here considered by the present writers that the deposits that contained this specimen are upper Gering and not Whitney, as recorded.

MINIOCHOERINAE, Subfamily 7

Miniochoerinae Schultz and Falkenbach, 1956, p. 391.

Discussion

Thorpe[1] referred an immature skull and mandible, S.D.S.M. 31133 ["311"], to *Merycoidodon culbertsonii* and considered the specimen to be one of three associated individuals, S.D.S.M. 28129, "a mother and foetal twins."[2] The skull with dI^1–dP^4 (dP^1 absent) and mandible with dI_1–dP_4 (dP_1 absent) were collected by George E. Osterhaut about 1890 from Tertiary deposits some 50 miles east and north of Greeley in Weld County, Colorado.

Scott[3] also referred this same specimen (S.D.S.M. 31133 ["311"]) to *Merycoidodon culbertsonii* but did not connect the individual with the three associated specimens mentioned above.

Scott did not mention the locality from which S.D.S.M. 31133 was derived. Thorpe, in considering the immature specimen S.D.S.M. 31133 as one of three associated individuals, must have thought that it was from South Dakota. Actually the specimen was collected in Colorado, although its geologic occurrence is unknown. No doubt it came from the Brule Formation. The skull and mandible are exceptionally well preserved. The fan-shaped occipital region of this skull is definitely similar to examples of the Miniochoerinae. In the Merycoidodontinae, the occipital wings are produced posteriorly and not widely spread.

Morton Green suggested (before the writers had seen the example) that the specimen was referable to the Miniochoerinae. (See p. 435 for discussion of Green's conversation and letter; p. 434 for discussion of Thorpe's report; and p. 435 for Scott's conclusions.)

The very young specimen S.D.S.M. 31133 is actually too young for generic identification. There is no doubt that it is referable to the subfamily Miniochoerinae. The specimen is of importance because it shows no indication of either dP^1 or dP_1. (See p. 29 for further evidence that oreodonts did not have deciduous dP^1 or dP_1.)

[1] 1937, p. 55, pl. 2, figs. 3, 4.
[2] Hernon, 1930, p. 259; O'Harra, 1930, p. 341.
[3] 1940, p. 656, pl. 70, figs. 1, 1a, and 1b.

OREONETINAE, Subfamily 8[4]

Oreonetinae Schultz and Falkenbach, 1956, p. 453.

BATHYGENYS Douglass

Bathygenys Douglass, 1901b, p. 256. Schultz and Falkenbach, 1956, p. 464.

Discussion

Additional material collected at Bates Hole, Wyoming, since 1956, has added much information concerning the characters of *Bathygenys alpha* and other species referable to the subfamily Oreonetinae. It is now evident that the occipital region is fan-shaped, the bulla inflated, and the orbit closed posteriorly. The holotype of *B. alpha* is a partial ramus from Pipestone Springs, Montana. The previously referred specimens included a partial maxilla and three partial mandibular rami from Pipestone, and a partial skull and mandible with partial skeletal elements from Bates Hole, Wyoming. These were recorded in the 1956 report by Schultz and Falkenbach.

Many additional specimens have been col-

[4] Dr. John A. Wilson (communication to C. Bertrand Schultz, 1964) reported that "The Capote Mountain Tuff [DeFord, 1958], early Chadronian, has produced a considerable number of *Limnenetes* and a larger oreodont now being studied by John A. Wilson, University of Texas." This is a new distribution record for the genus.

lected by Morris F. Skinner, Ted Galusha, and their associates.[1] In a study of this additional material, the following became obvious: the collection included (1) by far the most complete example of *B. alpha*; (2) a partial skull and mandible that possessed a much larger dental series, especially C/ and P_1, than had been known (*Megabathygenys goorisi,* new genus and species); (3) a partial skull similar to skulls of *B. alpha* but exhibiting a larger lacrimal bone and a deep lacrimal fossa (*Parabathygenys paralpha,* new genus and species): and (4) mandibular rami that are very shallow and possess unusually light dentitions (*B. alpha hedlundae*). These are described and discussed in the following pages.

1. *Bathygenys alpha* Douglass, referred from Natrona County, Montana. ("Zone B" of Chadron formation.)

EXAMPLE: Skull, F:A.M. 72336. Figure 46.

1a. *Bathygenys alpha hedlundae,* new subspecies, from Natrona County, Wyoming. ("Zone B" of Chadron.)

HOLOTYPE: Partial mandible, F:A.M. 72377. Figure 46.

2. *Megabathygenys goorisi,* new genus and species, from Natrona County, Wyoming. ("Zone B" of Chadron.)

HOLOTYPE: Partial skull, F:A.M. 72385. Figure 46.

3. *Parabathygenys paralpha,* new genus and species, from Natrona County, Wyoming. ("Zone B" of Chadron.)

HOLOTYPE: Partial skull, F:A.M. 72388. Figure 46.

1. **Bathygenys alpha** Douglass, referred
From "Zone B" of Chadron Formation, Natrona County, Wyoming

Bathygenys alpha DOUGLASS, 1901b, p. 256, pl. 9, figs. 7, 8. SCHULTZ AND FALKENBACH, 1956, p. 465, fig. 12.

ADDITIONAL CHARACTERS[2]

SKULL: Orbit round and closed posteriorly; supraoccipital foramina with definite anterior grooves; bulla inflated; postoccipital region fan-shaped.

DISCUSSION

Morris F. Skinner, Ted Galusha, and associates have collected a large number of specimens referable to this species since our 1956 report. The skull shown in figure 46 is the best example of *Bathygenys* thus far found, and it demonstrates certain characters hitherto unknown (see table 17).

Forty-two additional specimens are here listed:

EXAMPLE

Partial skull with C/–P^2 rt. and P^3–M^3. (w)	F:A.M. 72336	From oreodont faunal "Zone B" of Chadron, Middle Fork, Lone Tree Gulch, 35′ below ash D [D–35′],[3] Bates Hole, Natrona County, Wyoming; collected by Morris F. Skinner, Sr., Ted Galusha, and Marilyn Galusha, 1959 Figure 46

[1] Morris F. Skinner has provided Schultz with a chart showing the stratigraphic distribution of 10 volcanic ashes (A to J) inclusive at Lone Tree Gulch, Divide Area, and Blue Gulch in the Bates Hole collecting locality, Natrona County, Wyoming. The lowest ash, A, is 530 feet below the highest ash, J. All the specimens collected by Skinner and associates are tied in stratigraphically to the ashes. Schultz has included this precise stratigraphic information in brackets in the listings of the specimens, which seems appropriate since several potassium-argon dates are now available from Skinner's ash samples. The B ash zone has been dated as 33.3 million years ago, the intermediate ash zone, G, as 32.6 million years, and the uppermost ash zone, J, as 31.6 million years (Evernden, Savage, Curtis, and James, 1964). In the listings, "G-25′" means that the specimen was found 25 feet below the G ash zone, and so on.

[2] See Schultz and Falkenbach, 1956, p. 465.

[3] See footnote 1 above.

FROM "ZONE B" OF CHADRON, BATES HOLE, NATRONA COUNTY, WYOMING (COLLECTED BY MORRIS SKINNER AND TED GALUSHA PARTY)

FROM CENTRAL FORK, BLUE GULCH:

2 PARTIAL SKULLS		F:A.M.
Anterior portion of skull with C/–P^1 rt. and P^2–M^3 [G–30′]	(w‡+)	72337
Anterior portion of skull with C/–P^1 rt. and P^2–M^3 [G–35′]	(w)	72338
MAXILLA		
Partial left maxilla with M^1(br.)–M^3 [F+15′]	(w)	72339
2 MANDIBLES		
Partial right ramus and symphysis with P_1–M_1 (br.) and M_2–M_3 [G–25′]	(w+)	72340
Partial right ramus and symphysis with P_1–P_2 rt. and P_3–M_3(br.) [G–25′]	(w‡)	72341

FROM EAST FORK, BLUE GULCH:

MAXILLA AND MANDIBULAR RAMUS		
Right maxilla with P^2–M^3 and partial right ramus with P_1–P_2 alv. and P_3–M_3 [G–25′]	(w)	72342

FROM TRAIL FORK, BLUE GULCH:

SKULL		
Left anterior portion of skull with C/(rt.)–M^3 [G–25′]	(M+)	72343
MANDIBLE		
Partial mandible with P_1–M_3 [G–25′]	(w‡)	72344
5 MANDIBULAR RAMI		
4 partial left rami with		
P_4–M_1 rt. and M_2–M_3 [G–25′]	(w)	72345
M_2(br.)–M_3 [G–40′]	(w+)	72346
P_3–M_1 [G–25′]	(w‡)	72347
dP_4–M_1 [G–25′]	(I)	72348
Partial right ramus with P_2–M_3 [G–25′]	(M+)	72349

FROM WEST BRANCH OF BLUE GULCH:

MANDIBULAR RAMUS		
Partial left ramus with P_3(br.)–M_3 (M_1–M_2 rt.) [G–30′]	(w‡)	72350

FROM EAST BLUE GULCH:

MANDIBULAR RAMUS		
Partial left ramus with M_1(rt.)–M_3 [F]	(w‡)	72351

FROM SOUTH LONE TREE SIDE OF DIVIDE AREA BETWEEN BLUE GULCH AND LONE TREE GULCH:

2 MAXILLAE		
Partial left maxilla with P^3–M^3 [G–30′]	(w+)	72352
Partial left maxilla with dP^3(br.)–M^3 [G–20′]	(I)	72353

FROM DIVIDE AREA BETWEEN S. FORK OF LONE TREE GULCH AND BLUE GULCH:

2 MAXILLAE		
Partial left maxilla with M^1–M^3 [G–30′]	(w+)	72354
Partial right maxilla with M^1–M^3(germ, br.) [G–30′]	(I)	72355

		F:A.M.
MANDIBULAR RAMUS		
Partial left ramus with P_3–P_4 br. and M_1–M_2	(w+)	72356

FROM MAIN FORK OF LONE TREE GULCH:

2 MANDIBULAR RAMI		
Partial left ramus with M_2–M_3 [D–20′]	(w+)	72357
Partial left ramus with P_4–M_3 br. [D+6′]	(M+)	72358

FROM CENTRAL PART OF LONE TREE GULCH:

SKULL		
Anterior portion of skull with P^2–dP^3–M^3 [D–2′]	(I)	72359

FROM NORTH LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with P_3–M_3 [D–2′]	(w‡)	72360

FROM NORTH FORK OF LONE TREE GULCH:

MANDIBLE		
Partial mandible with /C–P_3 rt. and dP_4–M_3 (M_1 br.) [F]	(I)	72361

FROM SOUTH FORK OF LONE TREE GULCH:

2 MANDIBULAR RAMI		
Partial left ramus with P_4–M_3 (M_1 br.) [G–30′]	(M+)	72362
Partial right ramus with dP_4–M_3 [G–30′]	(I)	72363

FROM NORTH FORK OF LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with P_1–P_3 rt. and dP_4–M_2 [F]	(I)	72364

FROM "MIDDLE FORK" (=CENTRAL FORK), LONE TREE GULCH:

2 MAXILLAE		
Partial left maxilla with M^1–M^2 [F–10′]	(M+)	72365
Partial right maxilla with M^1–M^3 [D–2′]	(w+)	72366
4 MANDIBULAR RAMI		
2 partial left rami with		
M_1–M_3 br. [D–20′]	(w+)	72367
P_2–M_3 (M_1 absent) [F–10′]	(w‡)	72368
2 partial right rami with		
P_2–P_4 rt. and M_1(br.)–M_3 [F–10′]	(w)	72369
P_1–P_4 rt. and M_1–M_3 [F–10′]	(w+)	72370

FROM SOUTHWEST FORK OF LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial left ramus with P_1–P_4 rt. and M_1–M_3 (br.) [G–35′]	(w+)	72371

FROM LITTLE LONE TREE GULCH:

4 MANDIBULAR RAMI		
Partial left ramus with P_3(alv.)–M_3 (M_1 br.) [D–35′]	(w‡+)	72372
2 partial right rami with		
P_3–M_1 br. and M_2–M_3 [D+10′]	(w)	72373
P_3–M_1 [D–35′]	(w)	72374

FROM LEDGE CREEK:

2 MAXILLAE		F:A.M.
Partial left maxilla with M^1–M^2	(w)	72375A
Partial right maxilla with M^1–M^3(br.)	(w)	72375B

The above two maxillae appear to be from one individual.

MANDIBULAR RAMUS		
Partial left ramus with I_3–P_2 alv. and P_3–P_4	(w)	72376

1a. **Bathygenys alpha hedlundae,**[1] new subspecies

From oreodont faunal "Zone B" of Chadron Formation, Natrona County, Wyoming

Description

SKULL: (Unknown).

MANDIBLE: Mandibular ramus shallow, shallower than in examples of *B. alpha*.

DENTITION: Inferior dentition lighter than in species; premolars smaller than in species.

LIMBS: (Unknown).

MEASUREMENTS: Table 17 (p. 366).

ILLUSTRATION: Figure 46.

Discussion

The remains of *Bathygenys alpha hedlundae* consist of the inferior dentition only. The series are lighter and the premolars smaller than those found in any other oreodont. The form may actually represent a new genus.

The referred specimens are from various horizons in the Bates Hole area but do not show any change in size from the lowest to highest geologic occurrence, a condition similar to that found in examples of *Megabathygenys goorisi* and *Bathygenys alpha*.

Eight specimens are here recorded:

HOLOTYPE

Partial mandible with I_1–I_3 alv. and P_1(rt.)–M_2. (w‡) F:A.M. 72377 From oreodont faunal "Zone B" of Chadron, 25′ below ash G, South Fork, Lone Tree Gulch, Bates Hole, Natrona County, Wyoming; collected by Morris Skinner and Ted Galusha party, 1959

Figure 46

REFERRED FROM BATES HOLE, NATRONA COUNTY, WYOMING (COLLECTED BY MORRIS SKINNER, TED GALUSHA, CARL ELFGREN, ROBERT EMRY, AND MARILYN GALUSHA, 1958–1959)

FROM SOUTH FORK OF LONE TREE GULCH:

2 MANDIBULAR RAMI		F:A.M.
Partial left ramus with M_1–M_3 [G–20′][2]	(w‡)	72378
Partial right ramus with I_1–I_3 alv., /C–P_3 rt. and P_4 [D+20′]	(w+)	72379

FROM SOUTHWEST FORK OF LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial left ramus with dP_4–M_2 [G–35′]	(I)	72380

FROM NORTH FORK OF LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with I_2–P_1 rt. and P_3–dP_4–M_1 [D–25′]	(I)	72381

FROM CENTRAL FORK OF BLUE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with P_4(br.)–M_3 [G–25′]	(w+)	72382

FROM TRAIL FORK OF BLUE GULCH:

[1] Named in honor of Miss Caroline Hedlund, former secretary in the Frick Laboratory, who helped with the manuscript.

[2] See footnote 1, p. 383.

MANDIBULAR RAMUS		F:A.M.
Partial left ramus with I_2–P_4 rt. and M_1–M_2 [G–25′]	(M+)	72383

FROM DIVIDE AREA BETWEEN SOUTH FORK OF LONE TREE GULCH AND BLUE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with M_1–M_3 [F+40′]	(W)	72384

MEGABATHYGENYS, NEW GENUS

1. Megabathygenys goorisi,[1] new species

From "Zone B" of Chadron Formation, Natrona County, Wyoming

DESCRIPTION

SKULL: Moderately deep; slightly larger than in examples of *Bathygenys,* smaller than skulls of *Oreonetes* and *Limnenetes;* wide across the frontals; orbits closed posteriorly, roundish, similar to those of *Bathygenys;* muzzle wider than in last-mentioned genus.

MANDIBLE: Deep below alveoli border; symphysis deep, extending posteriorly to anterior border of P_4.

DENTITION: Superior teeth longer (anteroposteriorly) and wider (transversely) than in examples of *Bathygenys;* C/ and P_1 robust (somewhat more robust than in examples of *Bathygenys*); inferior series (except P_1) similar to that in *Bathygenus.*

LIMBS: (Unknown).

MEASUREMENTS: Table 17 (p. 366).

ILLUSTRATION: Figure 46.

DISCUSSION

The holotype and the two referred partial rami are the only examples of this genus and species. The superior dentition differs considerably in size from that in *B. alpha,* yet the lower series are similar except for a massive P_1. The P_1 of *B. alpha* is not known, but the root portions available suggest a comparatively smaller tooth.

It is possible that some of the mandibular rami referred to *B. alpha* may actually belong to this genus and species, in examples in which the P_1 and the symphysis area are not present.

Three specimens are here recorded:

HOLOTYPE

Anterior portion of skull with C/–M^3 (P^1 rt.) and partial left ramus with I_3–M_3 (P_2–P_3 alv.) (W‡+)	F:A.M. 72385	From oreodont faunal "Zone B" of Chadron, from below a channel deposit, 50′ above base of N. 3 section, 185′ below base of 350′ correlator ash,[2] W. side of Ledge Creek, No. 3 Wash, Bates Hole, Natrona County, Wyoming; collected by Morris F. Skinner, Ted Galusha, and associates, 1958 Figure 46

REFERRED FROM NATRONA COUNTY, WYOMING

FROM DIVIDE AREA BETWEEN SOUTH FORK AND LONE TREE GULCH:

MANDIBULAR RAMUS		F:A.M.
Partial right ramus with P_1–P_4 [G–30′] . . . . Referred on the basis of a massive P_1.	(W‡)	72386

FROM LITTLE LONE TREE GULCH:

MANDIBULAR RAMUS		
Partial right ramus with P_1(rt.)–M_2 (P_3 rt.) [D–34′]	(W+)	72387

[1] Named in honor of Raymond Gooris, artist, Frick Laboratory, who has helped with the art work in this revision and also with the editing.

[2] For stratigraphic position of 350′ correlator ash (= Saddle Ash) at Ledge Creek No. 2 section, see Skinner and Gooris (1966, fig. 3, p. 5).

PARABATHYGENYS, NEW GENUS

1. Parabathygenys paralpha, new species

From oreodont faunal "Zone B" of Chadron Formation, Natrona County, Wyoming

DESCRIPTION

SKULL: Approximate size of that of examples of *Bathygenys* and *Megabathygenys*, but with less depth; lacrimal bone comparatively large, with deep fossa extending posteriorly downward below orbit; orbit more oblong (anteroposteriorly) than in *Bathygenys* (roundish in latter genus).

MANDIBLE: (Unknown).

DENTITION: Approximately equal to that of examples of *Bathygenys;* C/ light, lighter than in *Megabathygenys.*

LIMBS: (Unknown).

MEASUREMENTS: Table 17 (p. 366).

ILLUSTRATION: Figure 46.

DISCUSSION

The new genus *Parabathygenys* is based on the presence of a deep lacrimal fossa which is absent from *Bathygenys* and is questionably developed in *Megabathygenys.* In the study of the various families of oreodonts, it has been noted that the position and development (including presence or absence) of the lacrimal fossae are important characters, and these appear to remain constant within a species. In many instances, this also is true in a genus or in a subfamily, and little or no changes are noted. Some phylogenetic lines, however, show changes in the positions and the sizes of the lacrimal fossae during development.

It is important to note that *Bathygenys alpha, B. a. hedlundae, Megabathygenys,* and *Parabathygenys* all have recorded examples which have been collected from approximately the same general geologic horizons in the Chadron. The fact eliminates the possibility that these forms represent members of the same phyla but in different portions of the geologic sequence.

The posterior portion of the skull of *Parabathygenys paralpha* is unknown. Perhaps the postoccipital region, the bulla, and the general shape and size of the posterior portion of the skull may also differ from these characters in *Bathygenys.*

One specimen is here recorded:

HOLOTYPE

Anterior portion of skull with C/(rt.)–M^3. (w)	F:A.M. 72388	From oreodont faunal "Zone B" of Chadron, 25′ below ash G, West Fork, Blue Gulch, Bates Hole, Natrona County, Wyoming; collected by Morris Skinner, Ted Galusha, and associates, 1959 Figure 46

EXPLANATION OF TEXT FIGURES 44–47

FIG. 44. Lateral, dorsal, and ventral views of skulls: *Brachycrus rusticus riograndensis,* new subspecies, holotype, F:A.M. 72326, from deposits equal in age to the lower part of the Sheep Creek, Santa Fe County, New Mexico; *Merchyus crabilli ziaensis,* new subspecies, holotype, F:A.M. 72329, from deposits equal in age to the Harrison Formation, Sandoval County, New Mexico.

Superior dentitions: *Ticholeptus hypsodus leadorensis,* new subspecies, F:A.M. 72334, from deposits equal in age to the upper part of the Sheep Creek, Lemhi County, Idaho; *Ticholeptus,* species undetermined, example, F:A.M. 72335, from deposits equal in age to the upper part of Sheep Creek, Humboldt County, Nevada.

Mandibular ramus and inferior dentition: *Merychyus crabilli ziaensis,* new subspecies, holotype, F:A.M. 72329, from deposits equal in age to the Harrison Formation, Sandoval County, New Mexico. ×½.

FIG. 45. Lateral, dorsal, and ventral views of skull, inferior dentition, and mandibular ramus of *Ustatochoerus profectus nevadaensis,* new subspecies, holotype, A.M. 32634, from deposits equal in age to the Lower Ash Hollow Formation, Elko County, Nevada. ×½.

FIG. 46. Lateral dorsal, ventral, and occipital views of skull of *Bathygenys alpha* Douglass, referred, F:A.M. 72336, from "Zone B" of the Chadron, Natrona County, Wyoming.

Lateral views of skulls: *Megabathygenys goorisi,* new genus and species, holotype, F:A.M. 72385, from "Zone B" of Chadron, Natrona County, Wyoming; *Parabathygenys paralpha,* new genus and species, holotype, F:A.M. 72388, from "Zone B" of Chadron, Natrona County, Wyoming; *Brachycrus laticeps mooki,* new subspecies, holotype, A.M. 21321, from deposits equal in age to the upper part of the Sheep Creek, Meagher County, Montana. ×½.

Superior dentitions: *Bathygenys alpha* Douglass, referred, F:A.M. 72336 (as above); *Parabathygenys paralpha,* new species, holotype, F:A.M. 72388 (as above); *Megabathygenys goorsi,* new species, holotype, F:A.M. 72385 (as above). ×1.

Superior dentitions: *Brachycrus vaughani rioosoensis,* new subspecies, holotype, F:A.M. 72328, from deposits equal in age to the upper part of the Sheep Creek, Santa Fe county, New Mexico; *Brachycrus laticeps mooki,* new subspecies, holotype, A.M. 21321, from deposits equal in age to the upper part of the Sheep Creek, Meagher County, Montana. ×½.

Mandibular rami: *Megabathygenys goorisi,* new species, holotype, F:A.M. 72385 (as above); *Bathygenys alpha hedlundae,* new subspecies, holotype, F:A.M. 72377, from "Zone B" of the Chadron, Natrona County, Wyoming; *Brachycrus,* species undetermined, example, F:A.M. 72327A, from deposits equal in age to the Sheep Creek, Lemhi County, Idaho. ×½.

Inferior dentitions: *Megabathygenys goorisi,* new species, holotype, F:A.M. 72385 (as above); *Bathygenys alpha hedlundae,* new subspecies, holotype, F:A.M. 72377 (as above). ×1.

Inferior dentitions: *Brachycrus,* species undetermined, example F:A.M. 72327A, from deposits equal in age to the upper part of the Sheep Creek, Lemhi County, Idaho; *Brachycrus,* species undetermined, example, A.M. 55598, from deposits equal in age to the upper part of the Sheep Creek, Elko County, Nevada. ×½.

FIG. 47. Lateral, dorsal and ventral views of skulls: *Desmatochoerus (Paradesmatochoerus) anthonyi,* new species, holotype, F:A.M. 72392, from Gering Formation, Goshen County, Wyoming and questionably referred, F:A.M. 72393, from ?Gering Formation, Goshen County, Wyoming.

Mandibular rami and inferior dentitions: *D. (P.) anthonyi,* holotype, F:A.M. 72392 (as above); *Merychyus (Metoreodon),* species undetermined, example, F:A.M 72333, from deposits equal in age to the Sheep Creek, Santa Fe County, New Mexico.

Superior and inferior dentitions of *M. (M.),* species undetermined, example, F:A.M. 72389, from deposits equal in age to the upper part of the Sheep Creek, Lemhi County, Idaho. ×½.

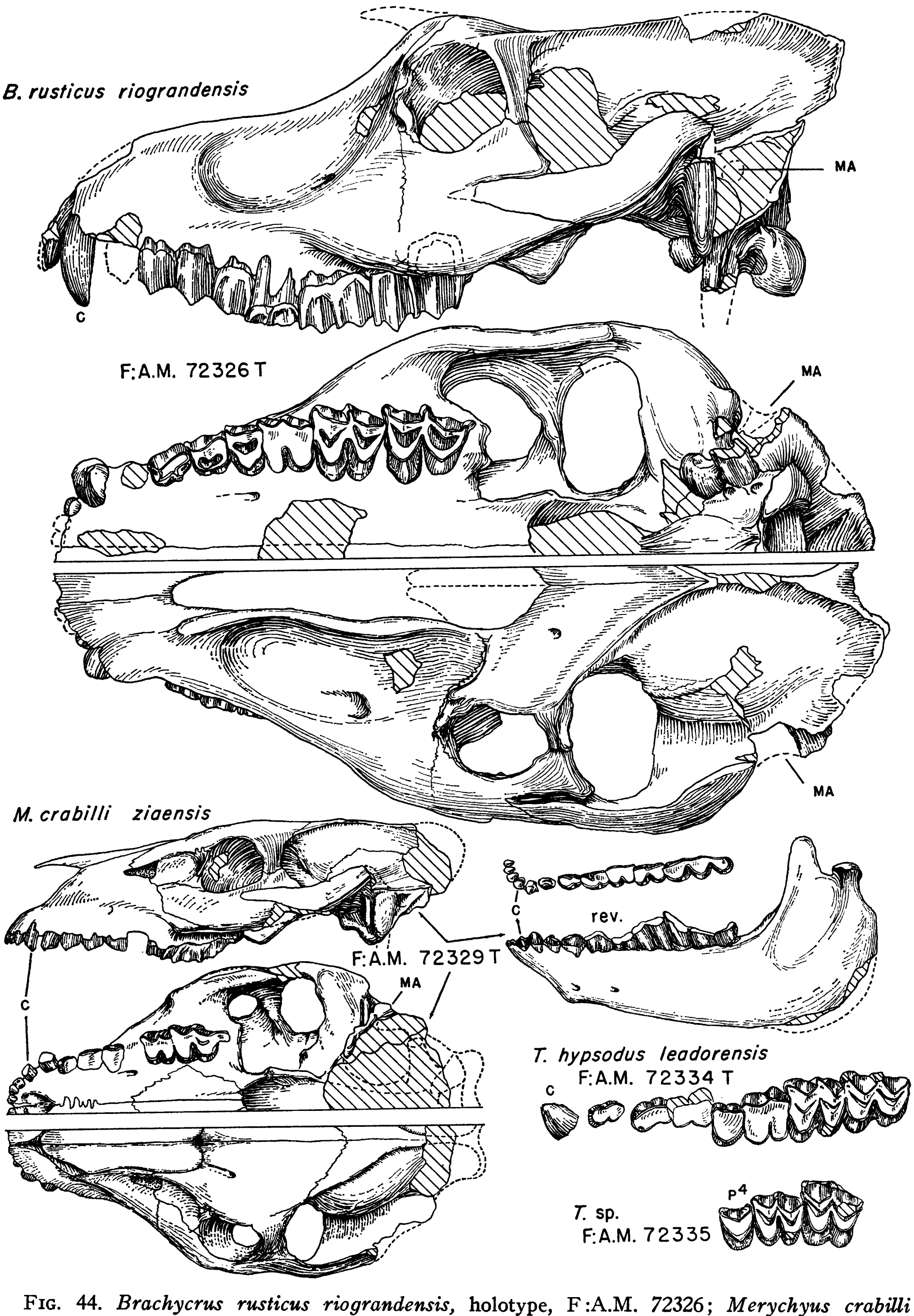


FIG. 44. *Brachycrus rusticus riograndensis,* holotype, F:A.M. 72326; *Merychyus crabilli ziaensis,* holotype, F:A.M. 72329; *Ticholeptus hypsodus leadorensis,* holotype, F:A.M. 72334; *Ticholeptus,* spec. undet., example, F:A.M. 72335. (See p. 389.) ×½.

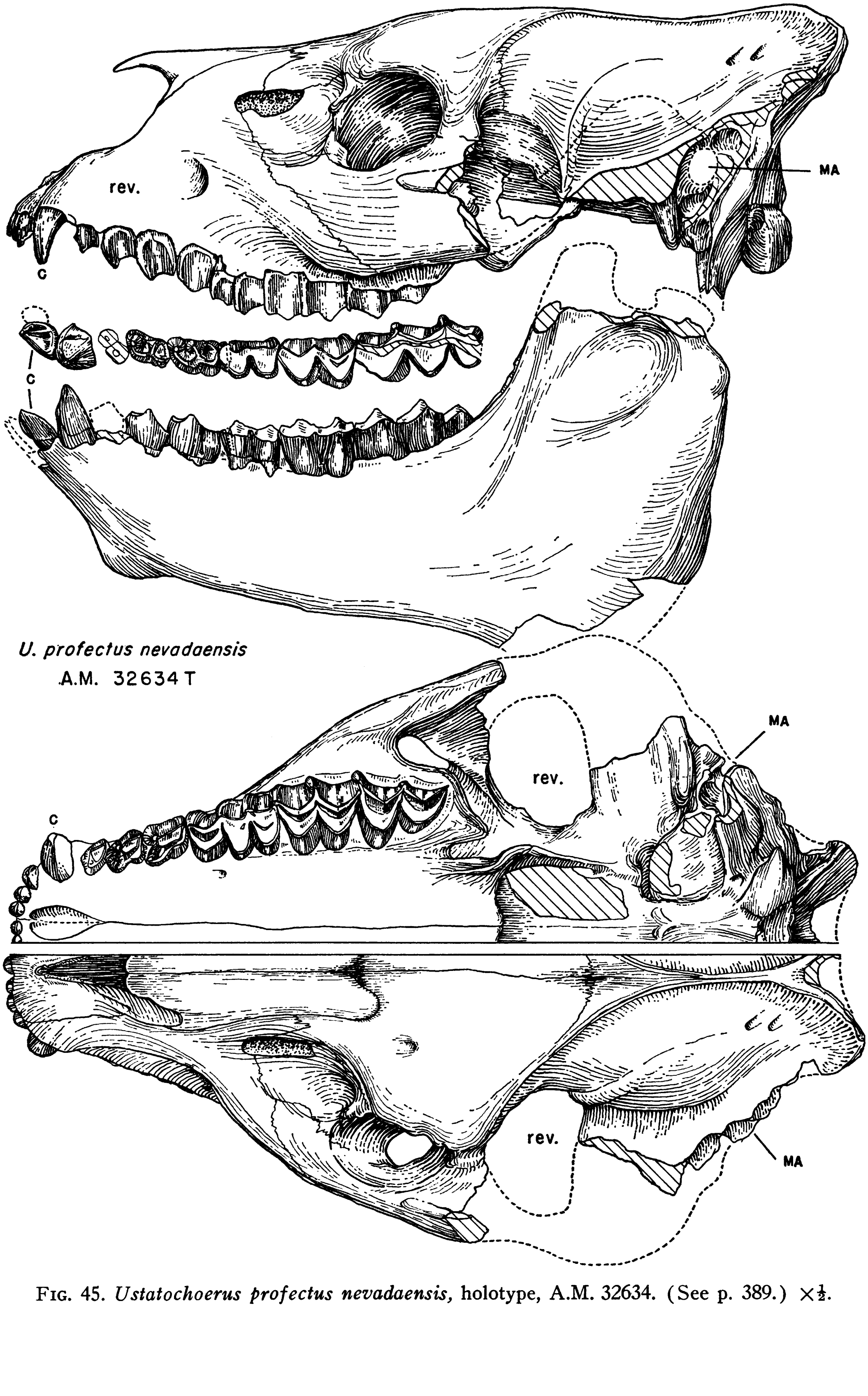


FIG. 45. *Ustatochoerus profectus nevadaensis,* holotype, A.M. 32634. (See p. 389.) ×½.

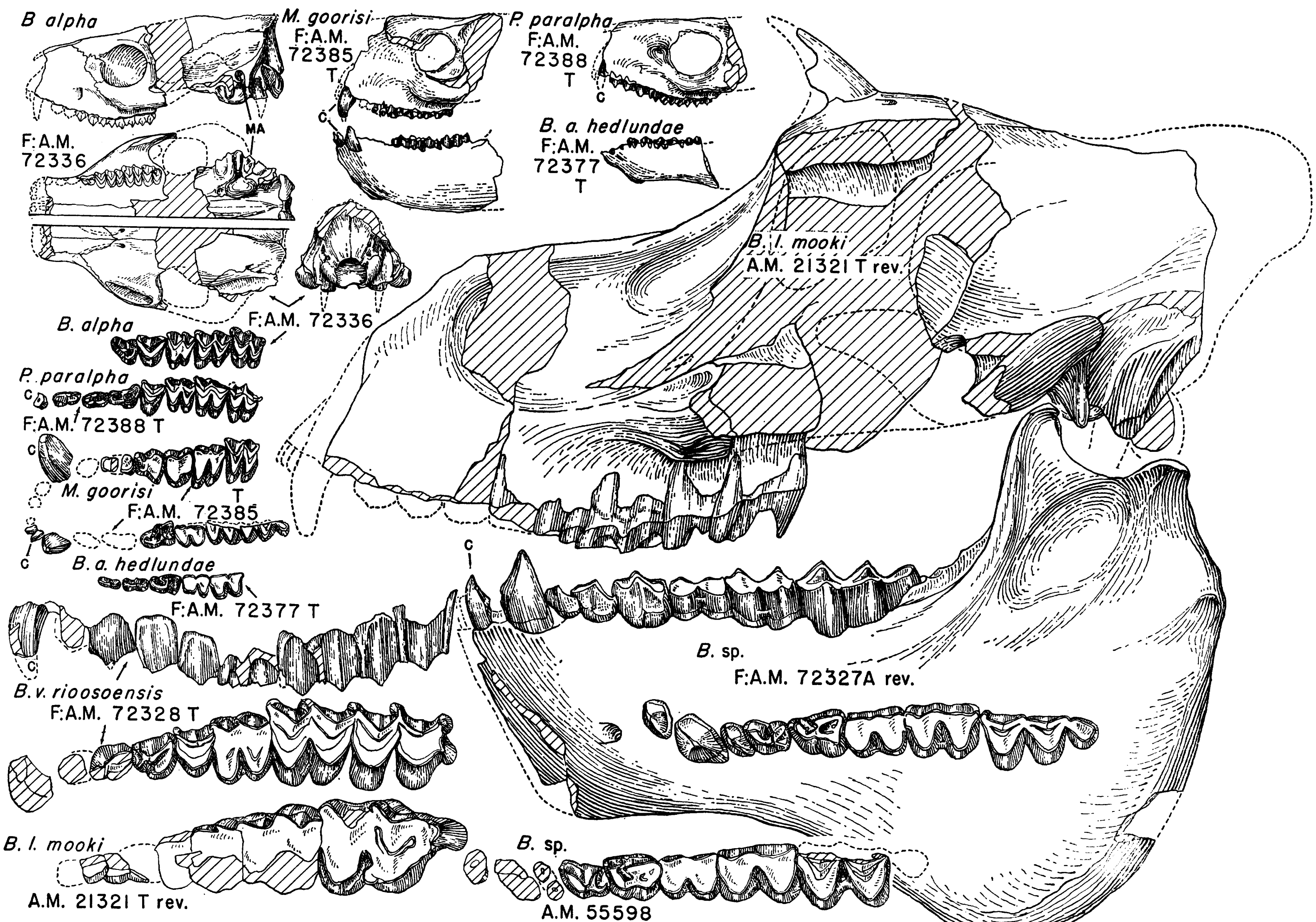


FIG. 46. *Bathygenys, Megabathygenys, Parabathygenys,* and *Brachycrus* holotypes, F:A.M. 72377, 72385, 72388, 72328, A.M. 21321, and referred, F:A.M. 72336, and examples, F:A.M. 72327A, A.M. 55598. (See p. 389.) ×½ (dentitions of *B. alpha, B. a. hedlundae, M. goorisi,* and *P. paralpha,* ×1).

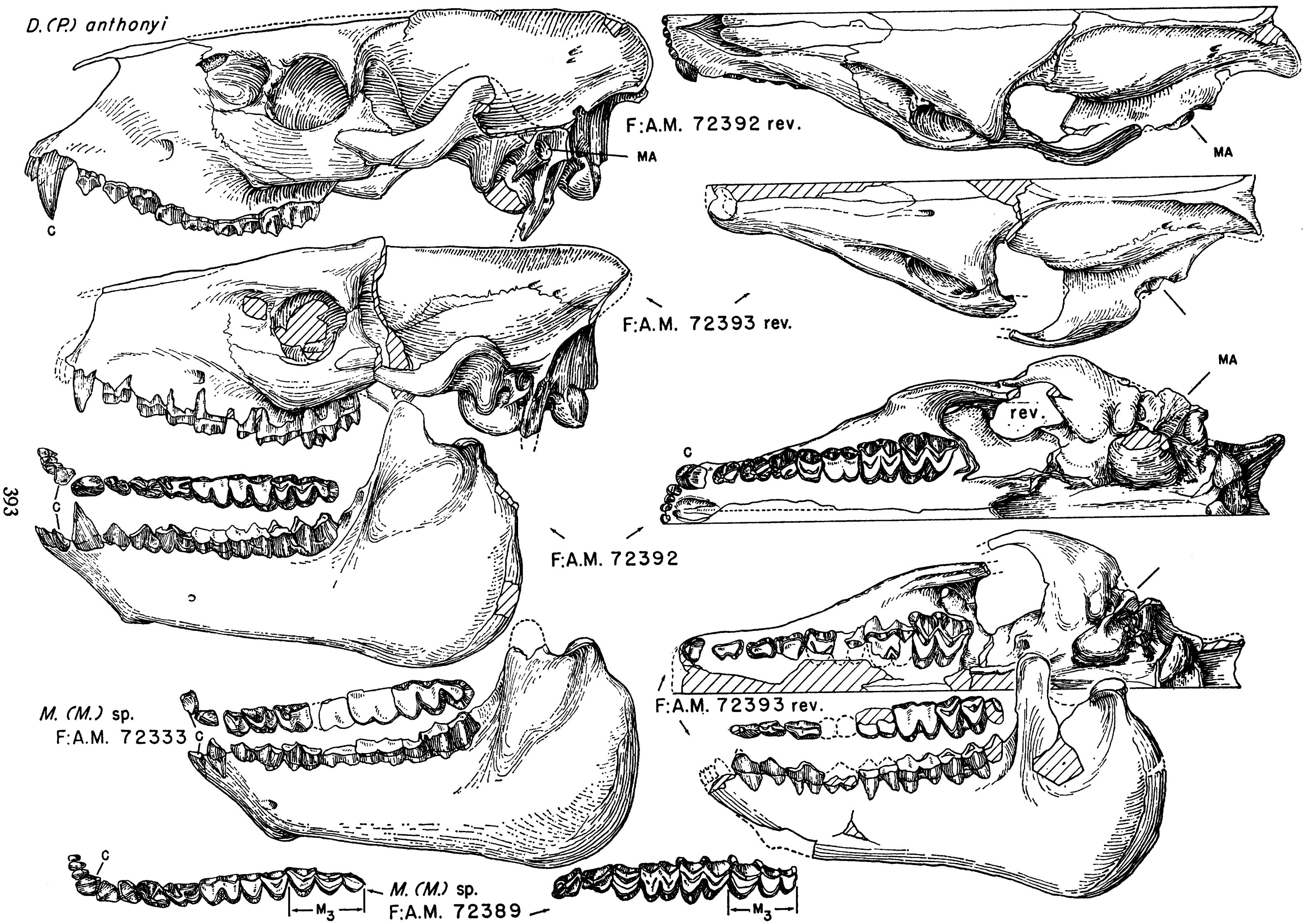


FIG. 47. *Desmatochoerus* (*Paradesmatochoerus*) *anthonyi*, holotype, F:A.M. 72392, and questionably referred, F:A.M. 72393; *Merychyus* (*Metoreodon*), spec. undet., examples, F:A.M. 72333 and 72389. (See p. 389.) $\times\frac{1}{2}$.

PART 2: SUMMARY AND CONCLUSIONS CONCERNING THE MERYCOIDODONTIDAE

INTRODUCTION TO PART 2

THE PRESENT REVISION of the oreodonts actually started during the spring of 1934 when Mr. Childs Frick asked the writers whether or not they would be interested in making a cooperative study of the genus *Promerycochoerus*. Dr. William King Gregory also advised C. Bertrand Schultz[1] to use some group of oreodonts as the subject for a doctoral thesis. A cooperative research project on the genus *Promerycochoerus* was agreed upon. Dr. Erwin H. Barbour, at that time Director of the University of Nebraska State Museum, also encouraged the proposed research work.

Neither of the present writers, at the time, suspected that the research would eventually result in a revision of the entire family Merycoidodontidae. When the project was under way, however, it soon became apparent to each of us that the genus *Promerycochoerus,* to which Hay[2] had referred 23 species, included many unrelated forms, so that consideration of other genera of the Merycoidodontidae was essential.

The writers have been fortunate in being able to see and study all the available type specimens of the family Merycoidodontidae. Such an opportunity has been a distinct advantage, and in many cases the original labels and field data associated with the types provided additional information or clues as to where the specimens had actually been collected. Field trips were planned and made to many of the areas of the various type localities. Additional specimens and geologic data were secured. Many of the areas were visited annually for many collecting seasons, thus bringing together a large assemblage of oreodonts, including many examples of one species.

The very large number of specimens representing different species have afforded many advantages: (1) a better understanding of individual variation (especially in cases in which the specimens came from fossil quarries representing a restricted period of geologic time); (2) knowledge of the vertical (geologic) change in forms, i.e., the change or variation of a species within a phylogenetic line; and (3) evidence of rapid changes or "breaks" in phylogenetic lines in the geologic sequence. This last evidence is well documented in the various phylogenetic lines that possess small (minute) bullae in oreodont faunal "Zone A" of the Brule and well-inflated ones in "Zone B." This evidence actually started a restudy of the White River deposits with the resultant recognition of a prominent paleosol (see chart 13) at the point in the geologic sequence which separates the specimens with the minute bullae below from the examples in the same phylogenic lines with the inflated bullae above. In this case it is evident that the paleosol complex represents a long period of time, at least enough to allow for considerable evolution of the bullae in at least two subfamilies of oreodonts (see chart 16).

Dr. Malcolm Thorpe, through his contribution "The Merycoidodontidae"[3] and the many discussions that the present writers had with him, was of considerable aid and encouragement. The much larger oreodont collections available to the writers, the greater amount of time available to carry on the research work in the field and laboratory, and the better stratigraphic evidence have led to conclusions different in many cases from those that Thorpe proposed.

The approach in the present revision differs from that of Thorpe in that the writers have used: (1) precise stratigraphic, as well as morphologic, evidence (see discussion, p. 401); (2) subfamily divisions; and (3) phylogenetic lines with genera and subgenera. The use of these three media has aided in establishing vertical phylogenetic lines rather than the lateral or horizontal grouping that has previously been used. The vertical lines show morphologic differences (including size) in a single genus between species or subspecies from various faunal zones. Previously many morphological differences in unrelated forms have been considered as individual variation within a single species or subspecies.

The geologic conclusions also vary from those of Thorpe, especially those concerning the John Day deposits. Thorpe[4] stated: "Whether this

[1] A graduate student at Columbia University during the spring semester of 1934.

[2] 1930, p. 1042.

[3] 1937.

[4] 1937, p. 8.

John Day Formation is upper Oligocene or lower Miocene is a mooted question which has led to much discussion. On the basis of the lithology and fauna, the writer considers the lower and middle John Day as upper Oligocene and the upper John Day as lower Miocene." In the present revision, however, all the John Day deposits that have yielded oreodont remains are considered to be Miocene. The lower John Day is known from flora only, and the oreodont fauna of the middle and upper John Day suggests that the deposits are equal in age to the Harrison Formation of the Great Plains, perhaps part of the upper John Day representing a portion of the hiatus between the Harrison and lower Marsland. (See chart 16, p. 420, for correlation of the various areas that have produced oreodonts.)

Thorpe further reported: "There is no sharp demarcation in the sedimentary record between the Oligocene and the Miocene, and yet in many localities there are indications of a long period of erosion, especially between the Monroe [Creek] and Harrison, and of the great environmental changes between these two epochs." The present writers believe that usually the division between Oligocene and Miocene is readily recognized. There is usually a noticeable unconformity dividing the sediments of the Oligocene from those of the Miocene, at least in the Great Plains region. There is also a decided lithologic difference between the sediments of the two geologic periods.

Thorpe also discussed the type of sediments in which oreodont remains are found and stated, "Of the fauna as a whole, the lowland forms were browsers, while those of the open country were more or less cursorial in type, such as the horses and camels." The further study of the oreodonts has not added greatly to this statement, except for a better understanding of the paleoecology associated with the leptauchenins (see p. 406) and the merycochoerins. Continued studies of the paleoecology of the Tertiary deposits will aid much in an interpretation of the habits of the various groups of oreodonts.

In the same publication Thorpe also reported: "In the Oligocene there was a short period of faunal interchange between Europe and North America which ended with the final phase of White River time. In the Deep River of the upper Miocene there was another interchange by the way of Siberia and Alaska, when the rhinoceroses and elephants came from Asia and Africa." The present writers doubt that the oreodonts migrated from the Old World,[1] i.e., as oreodonts. It is much more probable that the oreodonts developed from the Agriochoeridae in North America, but the actual relationship has not been established. Oreodonts are known only from North America. In fact, except for a few fragments from western Canada, all the known oreodont specimens have been found in the United States west of the Mississippi River. Such a range is unusually small geographically for a family of mammals that lived in such great numbers for such a long geologic period (early Oligocene to medial Pliocene). Undoubtedly the oreodonts had a wider range than this, but their remains have not been discovered, or perhaps preserved, in other parts of North America. The discovery of oreodont remains in the Panama Canal Zone in 1963 would certainly confirm this latter contention.

In 1899 Ameghino described a new species of mammal that he believed to be an oreodont. A portion of a palate with four molars was used for the holotype of *Diplotremus agrestis*. The palatal and side views of the teeth are plainly shown in Ameghino's illustrations. The molars, however, do not closely resemble those of any known oreodonts, and undoubtedly represent another example of convergence among the North and South American "ungulates." Thorpe[2] reported that "Ameghino seemed to consider it [*Diplotremus*] the South American equivalent of *Cyclopidius*," but Ameghino did not stress this point.

As to the geologic distribution of the proboscideans that Thorpe mentioned, the large Frick and University of Nebraska State Museum collections indicate that the earliest known remains of mastodonts in North America are from lower Pliocene deposits. It is here considered that all of the Ogallala, including the Valentine, or deposits of equal age are Pliocene. The only oreodonts known from the

[1] Certain European forms, such as *Caenotherium filholi* Lydekker, superficially resemble some of the oreodonts (see Cope, 1888, p. 1088, fig. 4).

[2] 1937, p. 23.

Pliocene belong to the genus *Ustatochoerus*. It was during the latter part of this period that the oreodonts became extinct.

Thorpe[1] considered that the Eocene genera *Protoreodon* (syn. *Eomeryx, Agriotherium*) and *Hyomeryx* and their reported species were all referable to the Merycoidodontidae. Gazin,[2] however, did not agree with Thorpe's conclusions and considered that *Protoreodon* (including *Eomeryx, Hyomeryx,* and *Agriotherium*) actually belonged to the Agriochoeridae. He stated, "From a review of all the types involved and much referred material, I have been led inescapably to the conclusion that *Protoreodon* as Peterson (1919, p. 82) indicated, was essentially an agriochoerid and not a merycoidodont."

The present writers some years ago measured most of the available Eocene "oreodonts" in various institutions, but decided not to include them in the present revision because these forms did not appear to be true oreodonts. In the Oreonetinae,[3] there remains the question of whether the orbits are open or closed posteriorly. Perhaps further research will disclose that some of the primitive merycoidodonts had open orbits.

The answer to the problem concerning the relationship between the Agriochoeridae and the Merycoidodontidae may rest in the recovery of specimens from lower Chadron (oreodont faunal "Zone A") deposits. A very small quantity of fossil material has been recorded from this portion of the Oligocene, and the writers have no knowledge of the occurrence of any diagnostic oreodont remains.

The 11 subfamilies of the Merycoidodontidae include 45 genera and 14 subgenera embracing 173 species and 35 subspecies. The oreodonts ranged in size from approximately that of a recent cottontail rabbit to that of a large domesticated pig. Unfortunately there are no living oreodonts, so it has been difficult to determine the degree of individual variation to be expected within a species. Therefore, the recent pigs, peccaries, antelopes, sheep, and other forms that resemble the oreodonts in various ways have been checked for individual variation, but no group contains the major variations (individual or otherwise) in the construction of the skulls that are found in the oreodonts. (See following discussion of dentitions, vacuities, and bullae.)

The oreodonts appear to be an ideal group for the study of evolution and the rate of change in the development of characters in various phylogenetic lines. Oreodont remains are preserved in large numbers, and the skulls, mandibles, and skeletal parts are frequently well preserved. The oreodonts were gregarious animals, hence frequently the fossilized remains of several individuals are found associated in the Tertiary rocks and thus provide evidence concerning individual variation.

Although the present writers have spent considerable time during the past 30 years on this research, they realize that further studies contributing to the knowledge of the geological history and the morphology of the oreodonts are necessary. Additional research work is needed in the following areas: (1) development and replacement of the milk dentitions; (2) brain casts; (3) skeletal elements (unknown in many species); (4) individual variation within species based on large associated assemblages; and (5) statistical analysis.[4]

Future workers undoubtedly will use precise stratigraphic data even more than have the present writers which will, of course, lead to even further "splitting" of the phylogenetic lines. Actually, in many instances there is some "lumping" in the present paper, chiefly because of an inadequate number of specimens or insufficient stratigraphic evidence upon which to base conclusions. This is especially true in the Eporeodontinae, because so few precise geological data are available in connection with the specimens examined.

Throughout the listings of the Frick Laboratory and the University of Nebraska State Museum material, the locality information has been shortened for convenience. If the precise field data associated with a particular specimen differ from the information (formation or faunal zone) of like specimens they are recorded in the listings. All information on published material is available either at the

[1] 1937, pp. 31–40.

[2] 1955, p. 47.

[3] 1956. Additional specimens since publication indicate that remains of *Bathygenys* possessed closed orbits. (See p. 382, and fig. 46.)

[4] See p. 437, present paper, for discussion of the statistical analysis of oreodont specimens.

Frick Laboratory or the University of Nebraska State Museum, depending on the specimens involved. In cases in which the geologic occurrence of holotypes is not known, it is always assumed that the holotype came from the same formation or faunal zone as did the referred examples.

Attention should be called to charts 13 through 17 of this paper, because they graphically summarize the general conclusions of the writers in regard to the classification, morphologic characters, stratigraphic distribution, and geographic occurrence of the oreodonts.

STRATIGRAPHIC AND MORPHOLOGIC APPROACH TO THE REVISION OF THE MERYCOIDODONTIDAE

THE PRESENT WRITERS have used the term "stratigraphic approach" in reporting on the revision of the oreodonts. It must again be clearly emphasized that this method of approach is strictly a consideration of both the precise stratigraphic occurrence of each specimen and its morphologic characters. Basing a study of fossils solely on either morphologic characters or precise stratigraphic evidence will not result in a natural phylogeny in any group under consideration. Taxonomy, phylogeny, variation, and geologic and geographic distribution have been stressed throughout this revision. The central Great Plains geologic section (see chart 13) has been the basis for faunal and geologic correlations, since the central Great Plains area is the only one in North America with a fairly complete stratigraphic sequence from lower Oligocene through upper Pliocene. Also the Great Plains section is well established and accepted by most workers who have collected in the area or who have made geologic studies there. The present writers have tried not to clutter up the reports with a multitude of geologic names; there are too many now for beds of approximately the same ages in the same region (see p. 411). Difficulties in interpreting geologic data associated with specimens often have been caused by collectors' going into an area that had previously been explored for fossils and then using nomenclature for the deposits and localities different from those that had previously been established.

The writers, in working with the oreodont remains, used a large table top (24 feet by 8 feet) that was divided into sections showing the geologic formations of the central Great Plains. Typical examples of oreodont skulls representing a subfamily were placed on the table according to their geologic occurrences. Then the similar morphologic characters from the different formational divisions were shifted in order to establish phylogenetic lines. A more critical consideration of the morphologic characters of the specimens from one faunal zone may indicate that one or several phyla were represented (see chart 19, p. 431, which provides a graphic summary of the phylogenetic lines of the Leptaucheniinae).

In order to interpret the morphologic characters of the oreodonts and establish a plausible taxonomic revision, the stratigraphic data must be associated with the specimens. It is true that in any collection, regardless of the collector, there are always a few specimens with field data that do not compare with other material collected. In these cases there usually are human errors, either in the interpretation of the geology, in the marking of the field data, or in the preparation laboratory. When such specimens are listed in the present paper, a notation appears below its listing.

The rates of development of the various phylogenetic lines differ considerably. This is graphically shown in charts 18 and 18a in the *Merycochoerus-Brachycrus* line, in which the phylogenetic development was rapid during the medial and late Miocene, and in that portion of the *Merychyus-Ticholeptus-Ustatochoerus* line, which demonstrated only minor morphologic changes during the same geologic time. Chart 19 also demonstrates various rates of evolution in six parallel lines of development in the Leptaucheniinae.

The present writers have spent much time in making geologic sections of the areas in which field parties from their respective institutions have collected. They have visited other localities where oreodonts have been found, and have studied the geologic records made by previous collectors. Special field conferences also were held with various geologists and paleontologists in order to clarify certain interpretations of field data. These field and conference experiences have aided much in the evaluation and correlation of the deposits in the various areas. The present report is a revision of the oreodonts based on stratigraphic evidence as well as morphologic characters. The writers are especially indebted to both Morris F. Skinner and Mylan Stout for providing stratigraphic data concerning the oreodont collections.

The present widely accepted division between the Chadron (top of "Zone C" of Chadron) and Brule (base of "Zone A" of Brule) is the "Purplish White Layer." In places this is represented by algal limestone layers. These are convenient field markers, and they have a widespread geographic distribution. It should be noted, however, that the oreodonts from "Zone C" of the Chadron and those from "Zone A" of the Brule within the same phylogenetic lines usually have similar morphologic characters. Usually there are no more than subspecific differences between the forms from these two different geological levels. In contrast to this faunal distribution, the oreodonts from "Zone B" of the Chadron differ considerably from those of "Zone C." There apparently was not a noticeable time break in deposition of deposits during the transition from Chadron to Brule times.

Perhaps the most important faunal break in the Oligocene occurs at the top of oreodont faunal "Zone A" of the Brule (= upper part of Middle Orella member). As has been pointed out previously, with the exception of the Miniochoerinae (in which the bullae remained small [minute]) and the Leptaucheniinae (in which the bullae were greatly inflated throughout their history), the bullae of all other oreodonts recorded from the Brule change from minute in "Zone A" to inflated in "Zone B" of the Brule. A prominent paleosol complex[1] appears at the top of oreodont faunal "Zone A" of the Brule, but it is non-fossiliferous. These paleosols apparently represent a long period of time, at least enough to allow for the development of the bullae from being minute to being inflated. This time may have represented tens or even hundreds of thousands of years, perhaps more. This buried soil complex makes a much better natural lithologic as well as faunal division in the Oligocene sediments in both Nebraska and South Dakota than the present one between the Chadron and Brule deposits. The present writers, however, do not propose to suggest a change in stratigraphic nomenclature, but wish to point out the importance of the faunal break and paleosol complex that appear at the top of the Middle Orella member of the Brule Formation. No doubt when the paleosols of the Miocene and Pliocene are better understood, they will provide clues for faunal breaks in instances where ordinary lithologic breaks or unconformities are not apparent. The paleosols or buried soils of the Oligocene have been very helpful in matters of stratigraphic correlation, and also have provided the necessary evidence for certain oreodont faunal breaks (see discussion of paleosols, p. 413).

It should be emphasized that, in the making of stratigraphic collections, the problem of facies should be kept in mind. Fossils may be found in deposits representing channel, flood plain, distant flood plain, and upland facies and still be of the same geologic age and formation. Fossils are not commonly found, however, in deposits representing the very distant flood-plain facies or in the associated paleosol complexes. In some localities, however, where aeolian deposition was rapid, the bones were preserved. A quick accumulation of loess and volcanic ash together with some colluvial material appears to have been responsible for the preservation of the bones. In deposits of this type, such as the "1st white layer" of Skinner, in the lower Miocene deposits on top of Sheep Mountain in Shannon County, South Dakota, the fossils are well preserved. Here the paleosols were not well developed, hence leaching did not alter the bones much after the initial burial. In areas where major paleosols occur, the "soil acids" have destroyed most of the fossil evidence.

One of the problems that has confronted the present investigators is the correlation of geologic deposits between distant localities. When the usual stratigraphic methods could not be applied, the writers had to assume that the deposits were approximately equal in age if the oreodont material from the two localities was of the same species or the specimens were of approximately the same stage of development. If examples representing several different phylogenetic lines at both localities were available, and the forms were similar in each case, then the assumed correlations were more plausible.

In the case of the John Day deposits, the examples of *Promerycochoerus* suggest that the sediments were approximately equal in age to the Harrison Formation of the Great Plains. The skulls of this genus from the uppermost deposits of the John Day, however, are larger and seem to be slightly more highly evolved. This difference, of course, may be in part the result of geographic distribution, but the writers believe that it may also indicate that the uppermost John Day deposits in Oregon are of

[1] Schultz, Tanner, and Harvey, 1955, pl. 4.

slightly later age than the Harrison sediments of the Great Plains.

The problem of correlating the oreodont-bearing deposits of Montana with those of the John Day of Oregon, and with those of the Great Plains, was difficult. J. LeRoy Kay, who has collected extensively in Montana, has taken Falkenbach on several occasions to the various Montana areas. This cooperative work has resulted in a large collection for the Frick Laboratory. These field trips have given the present writers a better understanding of geologic occurrence of the oreodonts from Montana.

The faunal lists from Montana by Kay, Fields, and Orr[1] do not correspond with those of Douglass and are not complete, at least as far as the oreodonts are concerned. Seventeen species and variants, including four of the species named by Douglass, were omitted from the lists of these writers. Many of the oreodonts that were included were mentioned by earlier names, which actually made the later names of the present writers synonyms. Proof was not offered for these decisions, so undoubtedly many of their conclusions are not valid.

It is noteworthy that, in the faunal list of Kay, Fields, and Orr, there are several instances in which the same species is included under two separate genera: *Limnenetes anceps* (p. 35) and *Oreonetes anceps* (p. 36); *Merycochoerus madisonius* (p. 38) and *Brachycrus madisonius* (p. 38). It is also of interest that the same writers considered *Mesoreodon chelonyx* (p. 34) as "Arikareean" in age (early Miocene) and the same species (p. 37) from another locality as "Barstovian" (late Miocene).

The present writers have expressed their opinions on chart 16 (p. 420) concerning the geologic ages of the various Montana localities that have yielded oreodont remains. Chart 16 should be compared with the evidence presented by Orr,[2] by Kay, Fields, and Orr,[3] as well as the chart in Kay, Fields, and Orr,[4] which was prepared by Fields.

To clarify the taxonomy and stratigraphic distribution of some of the Montana oreodonts recorded by Kay, Fields, and Orr, the names published by these authors, and the equivalent names (with proposed geologic occurrences) that are used by the present writers, are given in table 19.

[1] 1958, pp. 33–38.

[2] 1958, p. 31 (for Madison Valley Formation).

[3] 1958, pp. 33–38.

[4] 1958, p. 39.

The following previously recorded oreodonts from Montana were not included in the faunal list of Kay, Fields, and Orr (an asterisk indicates Douglass' types):

Ticholeptus zygomaticus Cope: Schultz and Falkenbach, 1941, p. 85.
Merychyus siouense Loomis, geological variety: Schultz and Falkenbach, 1947, p. 227.
Promerycochoerus latidens Thorpe, geological variety: Schultz and Falkenbach, 1947, p. 105.
Mesoreodon chelonyx wheeleri (Koerner): Schultz and Falkenbach, 1949, p. 145.
**Merycoides cursor* Douglass: Schultz and Falkenbach, 1949, p. 157.
Pseudomesoreodon rooneyi Schultz and Falkenbach, 1950, p. 130.
P. rolli Schultz and Falkenbach, 1950, p. 131
?P. boulderensis Schultz and Falkenbach, 1950, p. 132
**Megoreodon grandis* (Douglass): Schultz and Falkenbach, 1954, p. 168
**Desmatochoerus hatcheri* (Douglass): Schultz and Falkenbach, 1954, p. 186
D. hatcheri grinnelli (Koerner): Schultz and Falkenbach, 1954, p. 189.
D. newchicagoensis Schultz and Falkenbach, 1954, p. 192
?Pseudodesmatochoerus pariogenus (Cope): Schultz and Falkenbach, 1954, p. 211
**Subdesmatochoerus montanus* (Douglass): Schultz and Falkenbach, 1954, p. 219
Paramerycoidodon (*Gregoryochoerus*) *meagherensis* (Koerner): this report, p. 103
Sespia heterodon (Cope): this report, p. 252
Pithecistes brevifacies (Cope): this report, p. 268

In connection with the Tertiary deposits in Montana, White[5] published a paper on the Canyon Ferry area of Montana and recorded deposits as follows: "Lower Oligocene (Chadronian) . . . Middle Oligocene (Orellan) . . . Lower Miocene (Arikareean) . . . Middle Miocene (Hemingfordian) . . ." The "Lower Miocene (Arikareean)" localities include three areas in close proximity. White (p. 398) in reference to his locality 24LC18, stated: "About 200 feet of fine-grained, dense, buff sandstone, which weathers into nearly vertical cliffs, are exposed in this area (fig. 42). In texture and color these deposits very closely resemble the

[5] 1954, p. 395.

TABLE 19

COMPARISON OF TAXONOMIC NAMES AND STRATIGRAPHIC DISTRIBUTION OF MONTANA OREODONTS BY KAY, FIELDS, AND ORR WITH THOSE OF THE PRESENT AUTHORS IN THE REVISION OF THE MERYCOIDODONTIDAE

Kay, Fields, and Orr (1958)	Present Authors
Limnenetes anceps Douglass; "Oligocene; Chadronian-Whitneyan"; p. 35	*Oreonetes anceps* (Douglass); "Zone B" of Chadron; 1956, p. 458
Oreonetes anceps (Douglass); "Oligocene; Chadronian"; p. 36	Same as above
Merycoidodon gracilis Leidy; "Oligocene; Chadronian"; p. 35	*Miniochoerus* (*Paraminiochoerus*) *gracilis* (Leidy); "Zone A" of Brule; 1956, p. 413
Mesoreodon intermedius Scott; "Miocene; Barstovian"; p. 37	*Mesoreodon chelonyx* Scott; Gering equivalent; 1949, p. 140
M. chelonyx Scott; "Miocene; Arikareean"; p. 34	Same as above
M. chelonyx Scott; "Miocene; Barstovian"; p. 37	Same as above
Mesoreodon longiceps Douglass; "Miocene and Pliocene"; p. 38	*Pseudodesmatochoerus longiceps* (Douglass); Harrison equivalent; 1954, p. 207
Promerycochoerus minor Douglass; "Oligocene-Miocene; Whitneyan-Arikareean"; p. 37	*Promerycochoerus* (*Pseudopromerycochoerus*) *minor* (Douglass); Harrison equivalent; 1949, p. 124
P. ?minor (Douglass); "Miocene; ?Arikareean"; p. 37	Same as above
Promerycochoerus montanus (Cope); "Miocene; Arikareean"; p. 34	*P.* (*Pseudopromerycochoerus*) *montanus* (Cope); Harrison equivalent; 1949, p. 128
Promerycochoerus barbouri (Schultz and Falkenbach); "Miocene; Arikareean"; p. 37	*P.* (*Parapromerycochoerus*) *barbouri:* Schultz and Falkenbach; Harrison; 1949, p. 117
?Promerycochoerus (Douglass); "Oligocene; Chadronian-Whitneyan"; p. 35	*Promerycochoerus* Douglass; restricted to Harrison or equivalent; 1949, p. 93
Merycochoerus Leidy; "?Barstovian"; p. 37	*Merycochoerus* Leidy; restricted to Marsland; 1940, p. 277
Brachycrus altiramum (Douglass); "Miocene-Pliocene; ?Arikareean-Clarendonian"; p. 38	*Brachycrus altiramus* (Douglass); Sheep Creek equivalent; 1949, p. 228
Merycochoerus elrodi Douglass; as above; p. 38	*B. elrodi* (Douglass); Sheep Creek equivalent; 1949, p. 229
Brachycrus laticeps Douglass; "Miocene; Barstovian"; p. 37	*B. laticeps* (Douglass); Sheep Creek equivalent; 1949, p. 231
Merycochoerus madisonius Douglass; "Miocene-Pliocene; ?Arikareean-Clarendonian"; p. 38	*B. madisonius* (Douglass); Sheep Creek equivalent; 1949, p. 230
Brachycrus madisonius (Douglass); as above; p. 38	Same as above
Merycochoerus compressidens Douglass; as above; p. 38	*Ustatochoerus compressidens* (Douglass); Lowe; Ash Hollow equivalent; 1941, p. 15
Ticholeptus bannackensis Douglass; "Miocene; ?Arikareean"; p. 37	*Submerycochoerus bannackensis* (Douglass); Harrison equivalent; 1950, p. 127
Ticholeptus brachymelis Douglass; "Miocene and Pliocene"; p. 38	*Hypsiops brachymelis* (Douglass); Harrison equivalent; 1950, p. 116
Ticholeptus breviceps Douglass; "Miocene; ?Barstovian"; p. 37	*H. breviceps* (Douglass); Harrison equivalent; 1950, p. 120
Poatrephes paludicola Douglass; as above; p. 37	*Ticholeptus zygomaticus* Cope; Sheep Creek equivalent; 1941, p. 85
Ticholeptus smithi Douglass; as above; p. 37	*T. z. smithi* (Douglass); Sheep Creek equivalent; 1941, p. 86

Harrison deposits of western Nebraska and eastern Wyoming." It is not clear whether White considered these deposits equal to the Harrison formation in time since he did not state what Formation (Gering, Monroe Creek, or Harrison) the particular deposits may approximately equal in the central Great Plains.

Of particular interest to the writers is White's locality 24LC18; from this locality he reported remains of *Mesoreodon chelonyx*[1] Scott, *Promerycochoerus* [(*Pseudopromerycochoerus*)] *montanus*[2] Cope, and *Cyclopidius simus*[3] Cope. The Frick collections from the Canyon Ferry area include oreodont remains that are considered to be the equivalent of the Gering Formation in time. White's *Mesoreodon chelonyx* and *Cyclopidius simus* are here considered occurring in deposits equal to the Gering. However, *Promerycochoerus* (*P.*) *montanus* (Cope) is here considered as coming from beds equal in age to the Harrison.

In this connection White's[4] description is pertinent: "This specimen [*P.* (*P.*) *montanus*] is that of an old individual with the teeth well worn. However, the specimen is only slightly crushed and the size and configuration can be determined with reasonable certainty." This description allows one to conjecture that perhaps this "old individual" may belong to the species *Megoreodon grandis*[5] (Douglass). The illustration in White's figure 42 also suggests this possibility. It is possible that deposits of more than one geologic age are represented.

For further discussion of White's report, see the Leptaucheniinae (p. 301). Also for a discussion of the Smith River and Deep River locations, and the Deep River and Fort Logan formations, see page 403. Chart 16 (p. 420) indicates the approximate age of deposits included in the Deep River (= Smith River) location. Recent maps show Smith River, but most of the older geographic designations are "Deep River."

The writers do not use the available provincial time scale for the North American continental Tertiary[6] in the present contribution, because the Society of Vertebrate Paleontology Committee report on the "Nomenclature and Correlation of the North American Continental Tertiary" is presently being revised.

Two outstanding examples of the combination of the stratigraphic and morphologic approach are illustrated in charts 18 and 19. In chart 18, three examples of *Merycochoerus* are presented from three different parts of the Marsland Formation. Attention is directed to various characters that evolved rapidly through the comparatively short time interval during the deposition of the Marsland sediments, the formation to which *Merycochoerus* examples are restricted. (See explanation of chart 18, p. 427.)

In chart 19, the comparison is also based on both geologic occurrences and morphologic characters. In *Merycochoerus* there is apparently only one phylogenetic line which makes a clear, simple picture. However, in the Leptaucheniinae, there seem to be seven phyla, including 28 species and one subspecies. Without the consideration of the geologic occurrence in each instance and a careful screening of the morphologic characters, many different conclusions might be drawn. With all facts considered, the presented phylogeny is suggested. (See explanation of chart 19, p. 431.)

In reference to the genus *Merycochoerus*, the following report is timely. Wilson[7] discussed the geology and the occurrence of *Merycochoerus* and *Merychyus* in Colorado. The present writers wish to point out that they maintain, as published,[8] that remains of *Merycochoerus* are restricted to the Marsland formation of Schultz.[9] Wilson[10] also stated: "Further, *Merychyus elegans* is identified by Schultz and Falkenbach (1944, p. 192) as occurring in the Martin Canyon section and is classified as upper Marsland. This species almost certainly came from above the American Museum quarry [*Merycochoerus proprius magnus*] level. Specimens of *Merychyus* are, in fact, rather common at the level of Quarry A. However, the Quarry A beds are not so high to be later than

[1] Schultz and Falkenbach, 1949, p. 140 (= Gering Formation).
[2] *Idem*, 1949, p. 126 (= Harrison Formation).
[3] Present paper, p. 298.
[4] 1954, p. 395.
[5] Schultz and Falkenbach, 1954, p. 168 (six specimens from the Canyon Ferry area recorded).

[6] Wood and others, 1941.
[7] 1960, p. 13.
[8] Schultz and Falkenbach, 1940, p. 286; 1949, chart 1, p. 80.
[9] Schultz, p. 441.
[10] 1960, p. 14.

the 'upper Harrison,' if Cook and Gregory (1941, p. 549) are correct in maintaining that the Marsland of Schultz includes some distinctly later beds." Schultz agrees with Cook and Gregory that his Marsland includes (as stated by Wilson) "some distinctly later beds." The upper part of the Marsland includes Cook's[1] "Runningwater Formation." Schultz's original description of the Marsland formation included the old "Upper Harrison" as the lower part of the Marsland, and the "distinctly later beds" as the upper part of the Marsland (= "Runningwater").

As to Wilson's statement that examples of *Merychyus elegans* were from the upper Marsland, he admitted that the specimens "certainly came from above the American Museum quarry level [site of *Merycochoerus proprius magnus*]." The present writers certainly agree with Wilson that remains of *Merychyus elegans* came from the upper Marsland and those of *Merycochoerus proprius magnus* came from the middle Marsland.

As to the reference that "specimens of *Merychyus* are, in fact, rather common at the level of Quarry A," Wilson did not state whether these specimens were referable to *M. elegans* or to one of the lower Marsland forms, *Merychyus minimus* or *M. arenarum.*

Wilson also wrote, ". . . the beds containing this quarry [*Merycochoerus proprius magnus*] are locally separated by an unconformity from those of Quarry A." A local unconformity may not represent a long period of time. The *Merychyus* examples may be referable to *M. elegans,* as the material available to the present authors was either *M. minimus* or *M. arenarum* from the lower Marsland, or *M. elegans* from the upper Marsland. The range of the previously mentioned two species may include the middle Marsland and also may extend downward to include the lower Marsland.

In an explanation of his figure 4 (p. 14) Wilson stated: "Figure 4 relates Quarry A to the standard North American sequence as well to the section at Martin Canyon. I have placed the Quarry A and Marsland levels in the late Arikareean, rather than the early Hemingfordian, because the fauna in Martin Canyon is clearly an advanced phase of the underlying Harrison." It should be noted that no deposits of Harrison age are present in the Martin Canyon area, nor does the absence or presence of a genus in a particular formation, or its apparent relationship with a form above or below said formation, indicate a change in time such as from "early Hemingfordian" to "late Arikareean."

Wilson also cited " 'index fossils' of the Arikareean . . .: *Diceratherium, Entoptychinae, Oxydactylus, Stenomylus,* and *Syndyoceras. Parahippus* is the most advanced horse." The present writers refer the reader to page 458 of the present report for a discussion of the usage "primitive" and "specialized" [= advanced]. The "index oreodonts" are of value to field and research workers, because the present revision was made from a stratigraphic approach. There is no doubt that all other mammal families, when revised with a consideration of geologic occurrences, will include excellent index fossils.

It should also be noted that both of the present writers were familiar with the Martin Canyon area. Also both visited, with Wilson, this interesting locality. As to the European correlation, it seems more important first to reach an agreement within local areas such as the deposits of Colorado, Nebraska, and Wyoming.

PALEOECOLOGY

Paleoecology is gradually becoming a valuable tool to the vertebrate paleontologist. It is desirable for the paleontologist to learn as much as possible about conditions of the past in order to interpret more correctly the fossilized remains with which he is working. The fossils themselves provide some clues which may be of value. The type and degree of preservation or fossilization, the abundance of material, the manner of occurrence, and the lithologic characteristics of the fossiliferous deposits are all important factors in a proper interpretation of the conditions of the past.

The present writers agree with Harvey[2] that "paleoecology is not simply the science of ecology projected into past time." There is another dimension which only a study of geology will divulge. The present writers have always tried to be on the alert for paleoecologic evidence in the field, the place where research in paleoecology as well as paleontology begins. The mor-

[1] 1960, pp. 204–205.

[2] MS, a, p. 82.

phology of the fossilized remains of the animals may provide some evidence, but the deposits from which the fossils were derived provide most of the needed paleoecologic evidence. The preliminary petrographic and lithologic studies must be carried on in the field and each sample taken must be documented in detail, or there will be errors as far as the interpretation of the paleoecology is concerned. Harvey[1] helped clarify the meaning of the term "paleoecology" when he reported: "Paleoecology, as the word is frequently used and most profitably understood, is the study of ancient environments and not the study of the complex relationship between these environments and the contemporary organisms. It might be well if both ecologists and paleoecologists would recognize this difference." Most important in paleoecology is the establishment of the ancient environment.

Matthew[2] was interested in trying to interpret these prehistoric environments and was one of the first to suggest that the fossils found in the sandstones and the clays differ from one another, and that the former represented a forest fauna and the latter a plains fauna. He did not recognize, however, that frequently one type displaced the other when climatic conditions changed. Matthew[3] gave some reasons for regarding a great part of the White River Formation as being aeolian and of similar origin to the prairie loess of the Great Plains. This idea remained more or less a theory, however, until Wanless[4] reported on the sedimentation of the Oligocene deposits of South Dakota.

The interpretation of the paleoecological conditions that existed during late Oligocene and early Miocene times has aided the writers greatly in the study and interpretation of the leptauchenins. A restudy of the morphologic characters of the leptauchenins and a consideration of the changing ecological conditions have led the writers to the conclusion that the leptauchenins that belonged to the tribe Leptaucheniini lived in very arid, desert-like regions. These unusual oreodonts had been considered to be aquatic animals by many paleontologists, but evidence strongly indicates that they probably were not dependent on water for drinking.

[1] MS, a, p. 83.
[2] 1901.
[3] 1899a, p. 407.
[4] 1923, p. 189.

The paleoecological evidence also provided clues as to why the leptauchenins developed in the direction they did, and even why they became extinct.

The consideration of the Oligocene and Miocene buried soils, or paleosols, as stratigraphic "markers" by Schultz, Tanner, and Harvey[5] has greatly aided the study of the stratigraphic distribution of oreodont remains. Harvey[6] reported the distribution of oreodont remains in the Brule Formation of Sioux County, Nebraska, as follows:

	Percentage of Oreodonts
Upper Whitney	82.4% of 57 specimens collected
Middle Whitney	79.0% of 100 specimens collected
Lower Whitney	70.5% of 177 specimens collected
Upper Orella	22.5% of 418 specimens collected
Middle Orella	21.2% of 1140 specimens collected
Lower Orella	
Upper portion	35.0% of 100 specimens collected
Lower portion	9.3% of 1224 specimens collected

The collection, on which the oreodont distribution was based, was made for the University of Nebraska State Museum by Cyril Harvey and his associates, and consisted of the microfauna as well as the larger forms representing not only mammals but also birds, reptiles, and other forms. It is of interest to note that in the lowest deposits of the Brule, where fossils are very abundant, only 9.3 per cent of the specimens collected were identified as oreodonts. On the other hand in the highest deposits of the Brule, where fossils are comparatively scarce, 82.4 per cent of the specimens collected were oreodonts. It should be pointed out that rhinoceros remains were comparatively scarce (1.8%) in the lowest sediments of the Orella, whereas in the upper Whitney 8.8 per cent of the specimens collected were identified as rhinoceroses. The rhinoceroses were chiefly *Hyracodon,* and the oreodonts were mostly leptauchenins (tribe Leptaucheniini). A con-

[5] 1953; 1955, p. 1, fig. 2. This work was encouraged by Charles Falkenbach.
[6] MS, a, p. 69; MS, b, pp. 60–64, tables 5–7.

sideration of the type of sediments involved is helpful in understanding the distribution of fossils. The Lower Orella deposits are typical flood-plain sediments. Tychsen,[1] on the other hand, discovered that the Middle and Upper Whitney deposits were very "loess-like in character and may have been deposited on inter-stream divide areas, away from the flood areas proper." The animals that lived during the upper part of the Brule times certainly had unfavorable living conditions due to the blowing dust and the volcanic ash. Harvey[2] also reported: "Deposition [Middle and Upper Whitney] probably took place some distance from the region occupied by the main drainage stream, since there is no evidence of channel deposition in the area [northeast Sioux County]. Under such conditions it seems especially likely that both water and wind played their respective roles. Certainly the ash deposits indicate aeolian action of some sort." Most of the fossils found in the Middle and Upper Whitney sediments are enclosed in clay-siltstone nodules, which are cemented by calcium carbonate. The nodules must have been formed by the action of ground water. The vertebrate remains are usually well preserved, because the nodules are very resistant to weathering. The Leptaucheniini apparently were well adapted to the unfavorable climatic conditions of the late Oligocene and were able to survive in great numbers, but most of the other kinds of oreodonts either became extinct or lived in areas where the climate was more hospitable. Evidently the hyracodonts also had specialized in such a manner as to live in arid desert areas. Most of the other mammals must have found it difficult to survive, and migrated elsewhere, or lived along the banks of small streams that existed in the area at that time. The Leptaucheniini were well adapted for dwelling in deserts. The same was apparently true of the hyracodonts. As the climatic conditions changed at the end of Oligocene times and the beginning of the Miocene, and arid conditions no longer prevailed, the hyracodonts became extinct and the leptauchenins survived only for a short time during the early Miocene (see discussion on the habitats of the leptauchenins, p. 320).

There seems to be no evidence of examples of the tribe Sespiini in the Brule Formation or in any upper Oligocene deposits elsewhere (see chart 19). These curious tiny oreodonts suddenly appeared during earliest Miocene times and are best known from the Sespe deposits of California and the Gering of Nebraska and Wyoming. The Sespiini differ from the Leptaucheniini in that they possess unusually large orbits (see fig. 19) and very hypsodont molars (see fig. 42), both superior and inferior. The bullae of the Sespiini, although inflated, are not so prominent proportionately as those of the Leptaucheniini. Both *Sespia* and *Megasespia* perhaps were valley forms, since the remains are commonly found in channel deposits or in proximal flood-plain sediments of the Gering. It is difficult to speculate, however, on why the Sespiini had developed such hypsodont teeth since they apparently were valley or woodland forms, but their remains are not known from any deposits that suggest arid or desert conditions. Examples of the Leptaucheniini are usually found in the massive sediments representing the distant flood-plain and upland facies of the Gering. It is also questionable where the Sespiini species lived at the time the Leptaucheniini forms were so plentiful during the great drought periods of the late Oligocene when desert conditions prevailed in many parts of what is now the Great Plains region. The two tribes must have had ancestors in common early in the Oligocene. The two groups paralleled each other in general appearance to such an extent that Thorpe[3] selected an example (U.N.S.M. 28408, or field no. 2-26-7-32 SP), which the present writers consider to be the holotype of *Megasespia middleswarti*, and made it the plesiotype of *Leptauchenia decora* (see p. 256). An examination of the specimen clearly shows, however, that the resemblances are only superficial, for it has very hypsodont teeth, very weak external medial styles on the superior molars, and large orbits, all characteristic of the Sespiini.

The Sespiini have somewhat less prominent bullae than the lower Miocene Leptaucheniini, possibly because they were valley or woodland animals in contrast to the Leptaucheniini, which apparently were upland animals. It is of interest to note that the bullae of the Monroe Creek species of *Leptauchenia*, *Hadroleptauchenia*,

[1] MS, a, pp. 57, 82, 88.
[2] MS, a, p. 100.
[3] 1937, p. 235, figs. 1–4.

and *Pseudocyclopidius* have a tendency to be smaller than those of the ancestral Gering forms, perhaps as a slight adjustment brought about by ecological changes. Perhaps hearing was not so important to these animals as it was to their desert-living ancestors. There also was a tendency for the orbits to be larger (see chart 19) during late Gering and Monroe Creek times, another adjustment to the different environment. Seeing was more important to these animals than in the dusty uplands, where their ancestors had lived. Only in *Pithecistes* in the Leptaucheniini was there an indication of a larger bulla and no increased size of the orbits during Monroe Creek times. *Pithecistes* represented the most conservative line of the tribe (see chart 19), and apparently these animals continued to live in the driest regions available during the early Miocene. *Leptauchenia, Hadroleptauchenia,* and *Pseudocyclopidius* all apparently moved out toward the valleys, but probably preferred the uplands. These suggestions are based on field observations concerning the types of sediments in which the remains of the different genera are found. It must have been a considerable struggle for the Leptaucheniini to survive during early Miocene times, because of the vastly different climatic conditions which confronted them in contrast to the arid climate of the late Oligocene. The early Miocene must have been considerably more humid and the vegetation more luxuriant. This change in ecological conditions, of course, brought in a multitude of other mammals, including many species of oreodonts that were adjusted to a humid climate. The leptauchenins, which were the dominant animals of the late Oligocene, gradually decreased in importance during the early Miocene, finally becoming extinct during the Monroe Creek period of sedimentation. Apparently the competition from other kinds of oreodonts and other mammals, and the struggle to readjust to different ecological conditions, were too much to endure. Both the Leptaucheniini and the Sespiini became extinct at about the same time, geologically speaking.

The study of the sediments in which the remains of *Merycochoerus* and *Brachycrus* have been found also has provided paleoecological evidence which has aided the writers to understand better the development of these interesting oreodonts. Chart 18 (p. 427) shows five stages of development of skulls in the *Merycochoerus-Brachycrus* line, ranging in age from early medial Miocene times to late Miocene. The skulls represent *M. matthewi* from the Lower Marsland, *M. proprius magnus* from the Middle Marsland, *M. proprius proprius* from the upper Miocene, *B. wilsoni* from the Lower Sheep Creek [= "Sheep Creek" of Matthew], and *B. siouense* from the Upper Sheep Creek [= "Lower Snake Creek" of Matthew]. In the Lower and Middle Marsland deposits the remains of *Merycochoerus* are found chiefly in distal flood plains and upland deposits. Articulated skeletons are frequently found. These oreodonts must have been primarily plains forms. The remains of *Merycochoerus matthewi* and *M. proprius magnus* are rarely found in stream-channel deposits. In the Upper Marsland deposits, the remains of *M. proprius proprius* are found chiefly in the flood-plain deposits, but many specimens also are encountered in channel deposits. In the Sheep Creek deposits the remains of *Brachycrus* in the Great Plains region are derived chiefly from stream-channel deposits. Articulated skeletons and even individual bones are rarely if ever found in the flood-plain deposits, and the bones recovered from the channel deposits are not articulated. It appears to the writers that this evidence from the types of sediments and from the morphologic characters indicates that the oreodonts of the *Merycochoerus-Brachycrus* line slowly evolved from typical plains forms to river valley and forest animals during medial and late Miocene times. The shortening as well as the retraction of the nasals suggests the gradual development of a prominent proboscis. Perhaps the animal developed semi-aquatic habits similar to those of the tapirs today. Superficially *Brachycrus* must have closely resembled the modern tapir. Newly discovered evidence of *Brachycrus* from the Cucaracha Formation of the Panama Canal Zone[1] suggests that these oreodonts had successfully adapted themselves also to a tropical or semitropical climate.

In future reports on the oreodonts Schultz plans to include more detailed paleoecological evidence. Much can be learned about the habits as well as the development of these animals by a study of the deposits in which the fossilized remains were preserved.

[1] See p. 398 for a preliminary discussion.

DISCUSSION OF CHARTS 13–17, 17A, 17B, 18, 18A, AND 19

CHARTS 13 TO 19 help to clarify, graphically, the stratigraphic and morphologic approach to the revision of the oreodonts. The geologic information concerning the Tertiary deposits that have yielded oreodonts has been considered; also most of the areas have been visited by either one or both of the present writers in order to make stratigraphic collections and to study the geology. The geologic sequence of the central Great Plains, however, is used as a control, since it is the only fairly continuous section from lower Oligocene through upper Pliocene in North America which produces oreodont remains at essentially all horizons. Chart 13 is an ideal geologic section showing the chief stratigraphic units of the Tertiary of the central Great Plains. The various charts containing the geologic sequence throughout this revision are based on this section. One of the advantages of the central Great Plains section is that the formations may be observed within a comparatively small area in northwestern Nebraska, eastern Wyoming, and southwestern South Dakota. It should be noted that the present writers consider the Valentine to be Pliocene in age. (See explanation of chart 13, p. 411.)

The family Merycoidodontidae is a widely diversified group in size and general characters. Chart 14 graphically presents outline drawings of skulls typical of the 11 subfamilies, and shows the proposed subfamily relationships. The known geologic range of each subfamily is also indicated. (See explanation of chart 14, p. 416.)

Oreodont remains are known from middle Chadron through the middle portion of the upper Ash Hollow formations (Oligocene-Pliocene) of North America only. Chart 15 graphically shows the geologic range of each subfamily and the relative number of phyla.

As previously stated, deposits from outside the central Great Plains have been correlated with the central Great Plains section, with the use of both stratigraphic and faunal evidence. Chart 16 demonstrates the correlation of the various geographic areas that have produced oreodont remains. The correlations are based primarily on oreodont faunas from the various localities, but the stratigraphic evidence also is considered in each instance. The names, listed under the 13 states and under Canada, are strictly locality terms. These geographic localities are shown opposite the central Great Plains section to indicate only proposed correlations of the deposits at the localities, which in no way implies that the formational names used in this section should be applied to Texas, California, or even South Dakota. It does seem, however, that the formations are traceable with the use of stratigraphic techniques from western Nebraska into southwestern South Dakota, eastern Wyoming, and northeastern Colorado. Certainly the Ogallala deposits can be traced from western Nebraska southward into Kansas and Oklahoma. It is well to point out that on chart 16 the Pawnee Creek locality, for example, is listed in four places: opposite the Orella member (lower Brule), middle and upper Whitney (upper Brule), upper Marsland, and Valentine. Thus deposits in the Pawnee Creek area are not considered to be of one geologic age. Oreodont faunas are known from each of these different deposits.

The geographic distribution of the oreodonts is plotted on a map of western United States in chart 17. Geologic symbols are shown at the areas that have yielded oreodont remains. (Compare with charts 13 and 16.) The fragmentary evidence from Canada (see p. 36) has been omitted from the map as well as the reported "oreodont" incisor from Florida, which is here considered to be a peccary incisor. The rectangular area (surrounded with dashed lines) with numbers 1–24 in portions of Nebraska, South Dakota, and Wyoming has been enlarged and a supplemental list has been added for clarity (see chart 17a). This area has been the main source of oreodont remains.

Chart 18 is a graphic presentation of skulls of *Merycochoerus*, showing the phylogenetic development during medial Miocene times. Certain morphologic characters (length of premaxillae, position of nasals, position of external auditory meatus, size of skull) changed rapidly. Chart 18a, on the other hand, shows graphically the skulls in a line (*Merychyus-Ticholeptus-Ustatochoerus*) that was conservative and developed very slowly from early Miocene to medial Pliocene time.

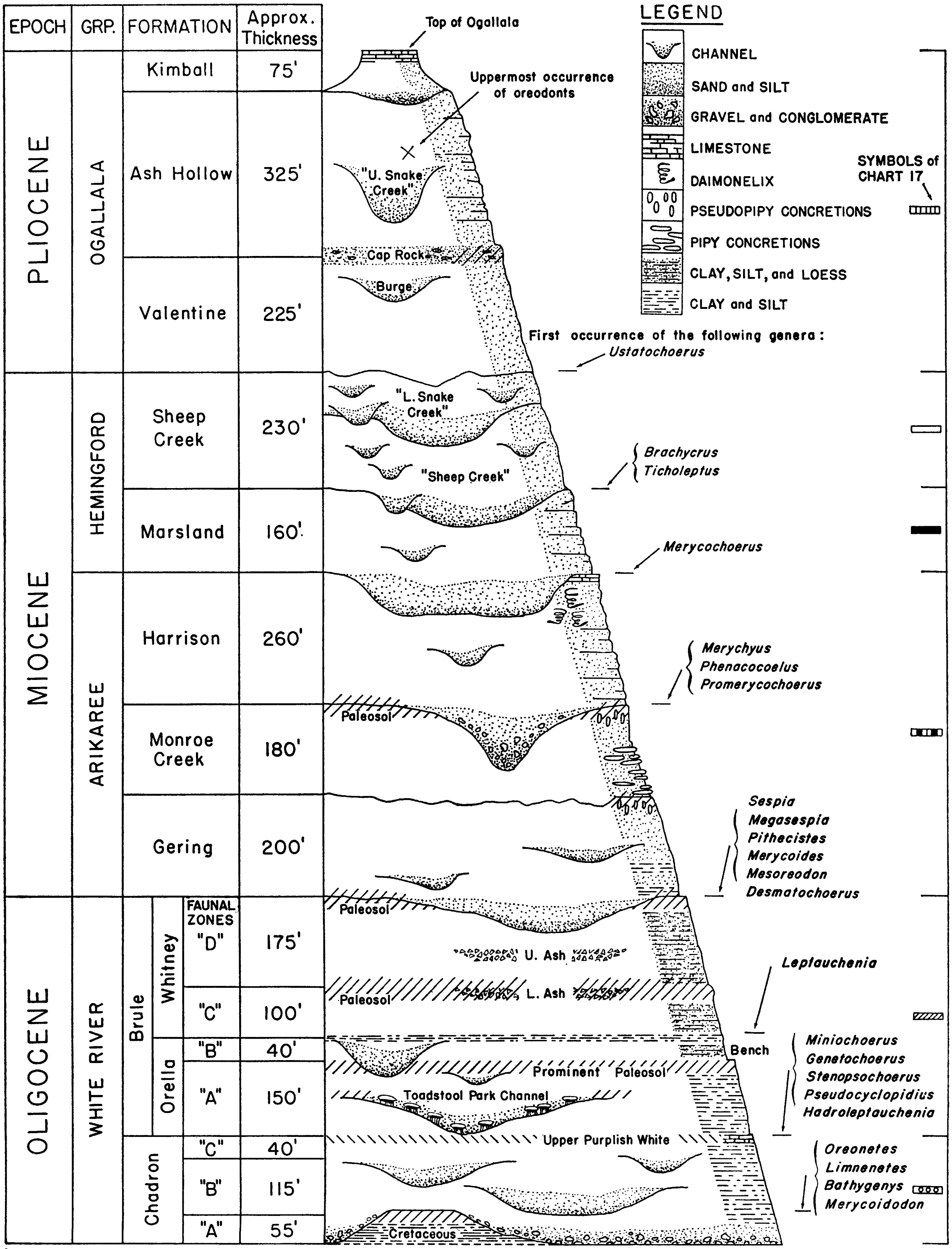


CHART 13. Ideal geologic section of the Oligocene, Miocene, and Pliocene deposits of the central Great Plains region, showing the chief stratigraphic units. The oreodont remains are found in deposits from middle Chadron to middle Ash Hollow. The first occurrences of various genera of oreodonts are indicated at the right of the section.

Chart 19 is a graphic summary of the development of skulls in the six phylogenetic lines of the Leptaucheniinae. It points out especially the superficial resemblances of parallel lines of oreodonts. Only with precise stratigraphic data associated with each specimen can the lines be split to this degree with any certainty. If the geologic information were not available, the specimens would have to be "lumped" into perhaps two or three lines.

EXPLANATION OF CHART 13

Chart 13 is the ideal section that has been accepted by various geologists and geological surveys as the standard geologic section for the middle and upper Tertiary deposits of the central Great Plains. Most fossil collectors who have made extensive stratigraphic fossil collections in the area have used this general section in its entirety or in part. This same sequence is used throughout the texts and in the geologic charts in the various contributions to the revision of the oreodonts. The origin of the nomenclature used in this geologic section follows.

OLIGOCENE

WHITE RIVER GROUP: Meek and Hayden[1] defined the White River as a "series" and also as "formations" and included younger formations now considered to be Miocene in age. Meek and Hayden[2] were more restrictive in their later definition, but the upper boundary of the White River was still indefinite. Wilmarth[3] considered the White River as a group and also a formation of "Oligocene (upper, middle, and lower)" age.

CHADRON FORMATION: Darton[4] defined the Chadron as a formation.

OREODONT FAUNAL ZONES OF THE CHADRON: The present writers have considered three faunal zones in the Chadron. The oreodont faunal zones "A," "B," and "C" are approximately equal in age to Osborn's[5] "Chadron geological horizons" A, B, and C. Clarke[6] named three members of the Chadron Formation, "Ahearn," "Crazy Johnson Butte," and "Peanut Peak" in southwestern South Dakota (these members are approximately equal in age to oreodont faunal zones "A," "B," and "C" of the Chadron).

Galbreath[7] named the "Horsetail Creek" Formation in northeastern Colorado (approximately equal in age to the oreodont faunal zones "B" and "C" of the Chadron).

BRULE FORMATION: Darton[8] defined the Brule as a formation.

ORELLA AND WHITNEY MEMBERS OF THE BRULE: Schultz and Stout[9] defined the Orella and Whitney as members of the Brule Formation.

OREODONT FAUNAL ZONES OF THE BRULE: Falkenbach and Schultz[10] originally proposed using oreodont faunal zones for the Brule as well as for the Chadron in order to avoid controversial stratigraphic correlations. However, much progress has been made in the field during the past 15 years in connection with various stratigraphic studies and correlations. Perhaps it will not be necessary to continue the use of the oreodont faunal zones in the future in the Colorado-Nebraska-Wyoming-South Dakota region. Oreodont faunal "Zone A" of the Brule equals the "Lower *Oreodon*" faunal zone of Wortman[11]; "Zone B" equals Wortman's "Middle *Oreodon*"; "Zone C" equals the "Upper *Oreodon*"; and "Zone D" equals the "*Leptauchenia* Zone."

Bump[12] named two members of the Brule in South Dakota, namely, the "Scenic" and "Poleslide." The "Scenic member" is approximately equal to the oreodont faunal zones "A" and "B" (also equal to the Orella member of the Brule in Nebraska), and the "Poleslide member" is approximately equal to the oreodont faunal zones "C" and "D" (also equal to the Whitney Member of the Brule in Nebraska).

Galbreath[13] named the "Cedar Creek" and "Vista" formations in northeastern Colorado.

[1] 1857, p. 117.
[2] 1861, p. 415.
[3] 1938, p. 2325.
[4] 1899a, p. 94; 1899b, p. 736; 1903a, p. 40.
[5] 1929, vol. 1, p. 57.
[6] 1954, p. 197.
[7] 1953, p. 12.
[8] 1899a, p. 94; 1899b, p. 736; 1903a, p. 37.
[9] 1938, p. 1921; 1941, p. 37; 1955, pp. 41, 44.
[10] 1951, p. 47; see also Schultz and Falkenbach, 1954, p. 154, chart 1.
[11] 1893, p. 95. See also Osborn and Wortman, 1894, p. 199; 1895, p. 343; Schultz, Tanner, and Harvey, 1955, p. 4; and Schultz and Falkenbach, 1961, p. 11.
[12] 1956, p. 429.
[13] 1953, p. 12.

The "Cedar Creek formation" is approximately equal to the Brule oreodont faunal zones "A" and "B" (also equal to the Orella member of the Brule in Nebraska), and the "Vista formation" is approximately equal to the Brule oreodont faunal zones "C" and "D" (also equal to the Whitney member of the Brule in Nebraska).

Schultz, Tanner, and Harvey[1] described certain Oligocene paleosols in Nebraska and South Dakota and indicated their stratigraphic positions in relation to the oreodont faunal zones. The paleosols have proved to be of great value in the correlation of Oligocene deposits over considerable distances, i.e, between Nebraska and South Dakota, and between Nebraska and Wyoming as well as Colorado.

Schultz and Stout[2] referred to the following divisions of the Chadron and Brule: Chadron divisions A, B, and C (= Osborn's "geologic horizons" A, B, C of the Chadron, also equal to oreodont faunal zones "A," "B," and "C" of the Chadron); Orella (lower Brule) divisions A, B, and C (= oreodont faunal "Zone A" of Brule); Orella (lower Brule) division D (= oreodont faunal "Zone B" of Brule); Whitney (upper Brule) division A (= oreodont "Zone C" of Brule); and Whitney (upper Brule) divisions B and C (= oreodont "Zone D" of Brule).

The United States Geological Survey[3] recognized the White River in "Wyoming, North Dakota, South Dakota, eastern Montana, Nebraska, northeastern Colorado"; the Chadron from "Western Nebraska and South Dakota, eastern Wyoming, and northeastern Colorado"; and the Brule from "Western Nebraska and South Dakota, northeastern Colorado, eastern Wyoming."

Miocene

Arikaree Group: Darton[4] described the Arikaree as a formation. Hatcher[5] divided the Arikaree into "The Monroe Creek Beds" and "The Harrison Beds." Schultz[6] proposed that the Arikaree be considered a group and include the Gering Formation as well as the Monroe Creek and Harrison.

Gering Formation: Darton[7] described the Gering as the formation immediately above the Brule and below the Arikaree. Darton[8] identified the Gering along Wildcat Ridge in the North Platte River drainage in Morrill, Banner, Scotts Bluff, and Sioux counties of Nebraska and along the north face of Pine Ridge in the White River drainage in both Dawes and Sioux counties, Nebraska. Harksen, Macdonald, and Sevon[9] proposed the name "Sharps formation" for the deposits "present between the Brule Formation of the Oligocene White River group below, and the Monroe Creek Formation of the Miocene Arikaree group, above." The "Sharps formation" includes deposits in Nebraska considered to be the Gering Formation in Nebraska by Darton.[10]

The present writers consider that the name "Sharps" is invalid, since both the faunal and stratigraphic evidence indicates that the deposits concerned are typical of the Gering Formation of Darton. Schultz and Stout[11] also do not regard the "Sharps" as a valid formation. Perhaps it could be considered a facies of the Gering Formation.

Cook[12] and later Cook and Cook[13] did not consider the Gering Formation as important and referred to the "Monroe Creek Beds" as "Basal Miocene," perhaps because the Gering fauna was still unknown as late as the early 1930's. Schlaikjer[14] included both the Gering and Monroe Creek deposits in the "Lower Harrison" in his studies of eastern Wyoming and western Nebraska. It is well to keep all these interpretations in mind when reading the literature concerned with both the Gering Formation and the Gering fauna.

Monroe Creek Formation: Hatcher[15] described the "Monroe Creek Beds" as the lower part of the Arikaree (see section on the Arikaree Group above).

[1] 1955, p. 3, fig. 1.
[2] 1955, p. 28.
[3] Wilmarth, 1938, pp. 278, 393, 2325.
[4] 1899a, p. 94; 1899b, p. 743; 1903a, p. 25.
[5] 1902, p. 115.
[6] 1938, p. 443.
[7] 1899a, p. 94; 1899b, p. 741; 1903a, p. 29.
[8] 1903a, pp. 30, 39, 40, pl. 20.
[9] 1961, p. 674, figs. 1–3.
[10] 1903a, pp. 30, 39, 40, pl. 20.
[11] 1961, p. 7.
[12] 1912, p. 39.
[13] 1933, pp. 28, 32.
[14] 1935, p. 111.
[15] 1902, p. 115.

HARRISON FORMATION: Hatcher[1] described the "Harrison Beds" as the upper part of the Arikaree (see section on the Arikaree Group above). Peterson[2] alter applied the name "Lower Harrison" to the entirety of Hatcher's "Harrison Beds," but most workers today use the original definition of the Harrison.

HEMINGFORD GROUP: Lugn[3] formally proposed the name "Hemingford" for the group and stated that it was a new division suggested by C. Bertrand Schultz. In 1938, Schultz,[4] in describing the Marsland, had left a blank on a geologic chart for the upper group of the Miocene, although "Hemingford Group" was a manuscript name that had been used by Schultz and Falkenbach[5] since 1936. The writers had urged Lugn to use the name "Hemingford" in his "Classification of the Tertiary System in Nebraska."

MARSLAND FORMATION: Schultz[6] proposed the name "Marsland" to replace the term "Upper Harrison" of Peterson,[7] since the so-called "Upper Harrison formation" was not a part of Hatcher's[8] Harrison. Cook[9] proposed to divide the Marsland into the "Upper Harrison" and a new formation, "Runningwater," but Schultz and Stout[10] refuted this classification. Wilson[11] included the Marsland in the Arikaree Group, but there is neither stratigraphic nor faunal support for such a classification. The present writers believe that the Marsland is definitely the lower part of the Hemingford Group both faunally and stratigraphically.

SHEEP CREEK FORMATION: Lugn[12] redefined the "Sheep Creek" and "Lower Snake Creek" of Matthew and Cook,[13] and included both in the Sheep Creek. Schultz and Falkenbach[14] have followed Lugn's redefinition throughout the present revision of the oreodonts, but have retained "Sheep Creek" and "Lower Snake Creek" in quotation marks as signifying the lower and upper members of the Sheep Creek Formation for the convenience of the readers, since much of the paleontological literature of western Nebraska refers to these terms. Hence "Sheep Creek" (in quotes) is used in the restricted sense by the present writers. Schultz and Stout[15] also considered the Sheep Creek, as redefined by Lugn, as a formation with two members. Certainly the "Sheep Creek" and "Lower Snake Creek" of Matthew and Cook are not mappable units, but faunal zones. The geology of the Sheep Creek-Snake Creek locality in Sioux County, Nebraska, is very complex, and recently has been studied and mapped in detail by Morris F. Skinner of the Frick Laboratory. This work has been of great value to the present writers in the study of the oreodonts from that area.

PLIOCENE

OGALLALA GROUP: Darton[16] described the Ogallala as a formation, and many workers still follow this designation, but the present writers consider the Ogallala as a group with three distinct mappable stratigraphic units. The faunal assemblages of these three formations are quite distinct one from another. Lugn[17] and Schultz and Stout[18] also have considered the Ogallala as a group with three formations: Valentine, Ash Hollow, and Kimball.

VALENTINE FORMATION: Barbour and Cook[19] described the Valentine, and Lugn[20] gave additional information on this formation.

ASH HOLLOW FORMATION: Engelmann,[21] in a United States Army report on the geology of the country between Fort Leavenworth, Kansas, and the Sierra Nevada, described the Ash Hollow Formation at Ash Hollow Canyon in western Nebraska. Lugn[22] later redefined the formation.

KIMBALL FORMATION: Lugn[23] described the Kimball in western Nebraska. This formation

[1] 1902, p. 115.
[2] 1906, p. 21.
[3] 1939b, p. 1253.
[4] 1938, p. 444.
[5] 1940, p. 220.
[6] 1938, p. 443.
[7] 1906, p. 21.
[8] 1902, p. 115.
[9] 1960, p. 204.
[10] 1961, p. 7.
[11] 1960, p. 1.
[12] 1939, p. 1255.
[13] 1909, p. 362.
[14] 1940, p. 220; 1941, p. 37; 1947, p. 232; 1949, p. 81.
[15] 1961, p. 8.
[16] 1899a, p. 94; 1899b, p. 734; 1903, pp. 16, 23.
[17] 1939, p. 1266.
[18] 1961, p. 9.
[19] 1917, p. 173; see also Lugn, 1939, p. 1259.
[20] 1939, p. 1266.
[21] 1876, pp. 260, 283.
[22] 1939, p. 1260.
[23] 1938, p. 220.

caps the Ogallala from Nebraska south to Texas and New Mexico. The Kimball is the only Tertiary formation (Oligocene through Pliocene) in which remains of oreodonts have not been found.

It should be noted that the thicknesses of the formations given on chart 13 are chiefly maximum ones, and that the thicknesses vary from one locality to another. Lugn and Lugn[1] used the following figures for the thicknesses of the Tertiary formations in Nebraska: Chadron, 50–190 feet; Brule, 500–600 feet; Gering, 200 feet; Monroe Creek, 275–360 feet; Harrison, 200–280 feet; Marsland, 80–200 feet; Sheep Creek, 25–200 feet; Valentine, 175–225 feet; and Ash Hollow, 100–250 feet.

EXPLANATION OF CHART 14

Chart 14 shows the stratigraphic distribution of the 11 subfamilies of oreodonts. The geologic correlations are based on the central Great Plains Tertiary section. The terms "Lower Snake Creek" and "Sheep Creek" are used in a limited sense (see chart 13, p. 411). The Brule oreodont faunal zones "A," "B," "C," and "D", and the Chadron faunal zones "A," "B," and "C," are used throughout this revision (see p. 401, also chart 13, p. 411).

The known geologic range of a subfamily is indicated by a solid line, with a horizontal bar at each end. A broken line indicates a possible relationship between subfamilies.

Outline drawings of the skulls are placed on the solid lines according to the formation in which the particular form occurred, in order to provide general size comparisons of the skulls of the various subfamilies. The shape of the occiput is indicated as follows: OFS, occipital region fan-shaped; OPP, occipital region posteriorly produced. The type of bulla is indicated as follows: B+, bulla inflated; B—, bulla minute; B+d, bulla inflated, with depressed area. The M³'s typical of each line are marked as follows: Br, brachyodont; Hy—, subhyposodont; Hy, hypsodont; Hy+, extremely hypsodont.

EXPLANATION OF CHART 15

Chart 15 is a graphic presentation of the limitations of the subfamilies of the Merycoidodontidae. The geologic section is of the Great Plains and is the one used throughout this revision. The graphic width of a subfamily is governed by the number of (vertical) generic and subgeneric lines at a given time within a subfamily (⅛ of an inch represents a phylogenetic line). The vertical limits are controlled by the geologic occurrences of subfamily examples. The lack of material from certain faunal zones is indicated by a broken line. The presence or absence of a genus or subgenus in a given faunal zone may indicate a true picture of occurrences, or may be due to the "luck" of collecting.

It is of interest to note that during the lower Miocene, when the Harrison sediments were deposited, oreodonts were very abundant. Representatives of six different subfamilies were living at that time, the greatest number for any one faunal zone. Not only did the oreodonts prosper in the midcontinent region of North America but also in the western part in what is now Oregon. Representatives of only one subfamily survived into the Pliocene.

EXPLANATION OF CHART 16

The apparent geologic correlation of deposits in various areas that have yielded oreodont remains is shown in chart 16. The geologic section used in this chart is that of the Great Plains and is the one used throughout this revision. It must be stressed that the locality names appearing on the chart do not represent local faunas or formations; therefore they are simply general locality names. The sizes of the spaces and lettering on the chart do not imply relative importance of one locality over the other. Lettering was sized according to the available space. It is also important to state that these correlations are based strictly on morphologic and stratigraphic evidence obtained from the study of the oreodonts, and that some of these localities may extend downward or upward in the geologic section, but only those portions are cited that have yielded oreodont remains. One locality may have oreodonts which have been recorded from several different stratigraphic levels, a fact that is well demonstrated in the Colorado area where the Pawnee Creek locality has deposits that are equivalent to the Brule, Marsland, and Valentine in age.

The chart also indicates the geologic range

[1] 1956, p. 100.

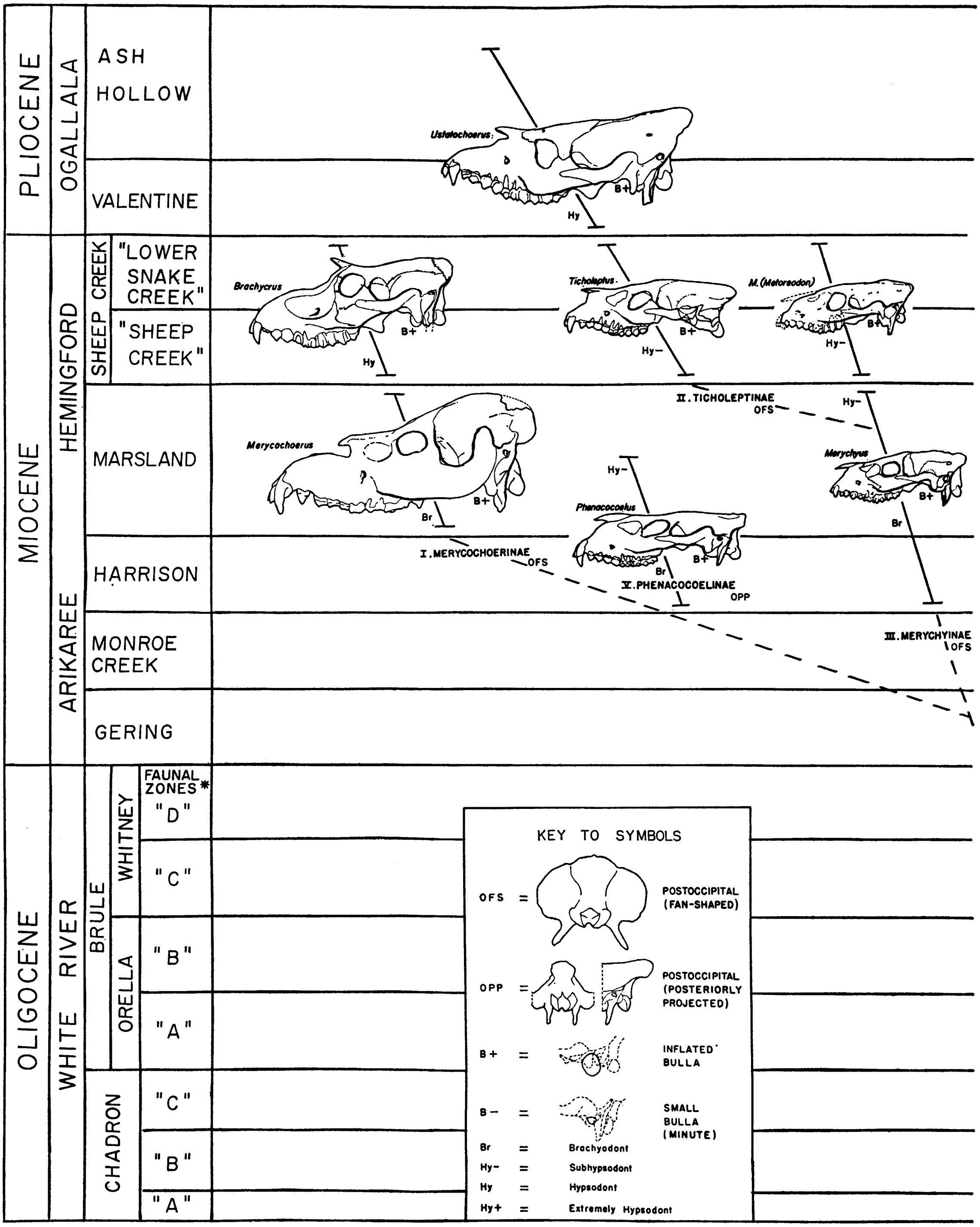
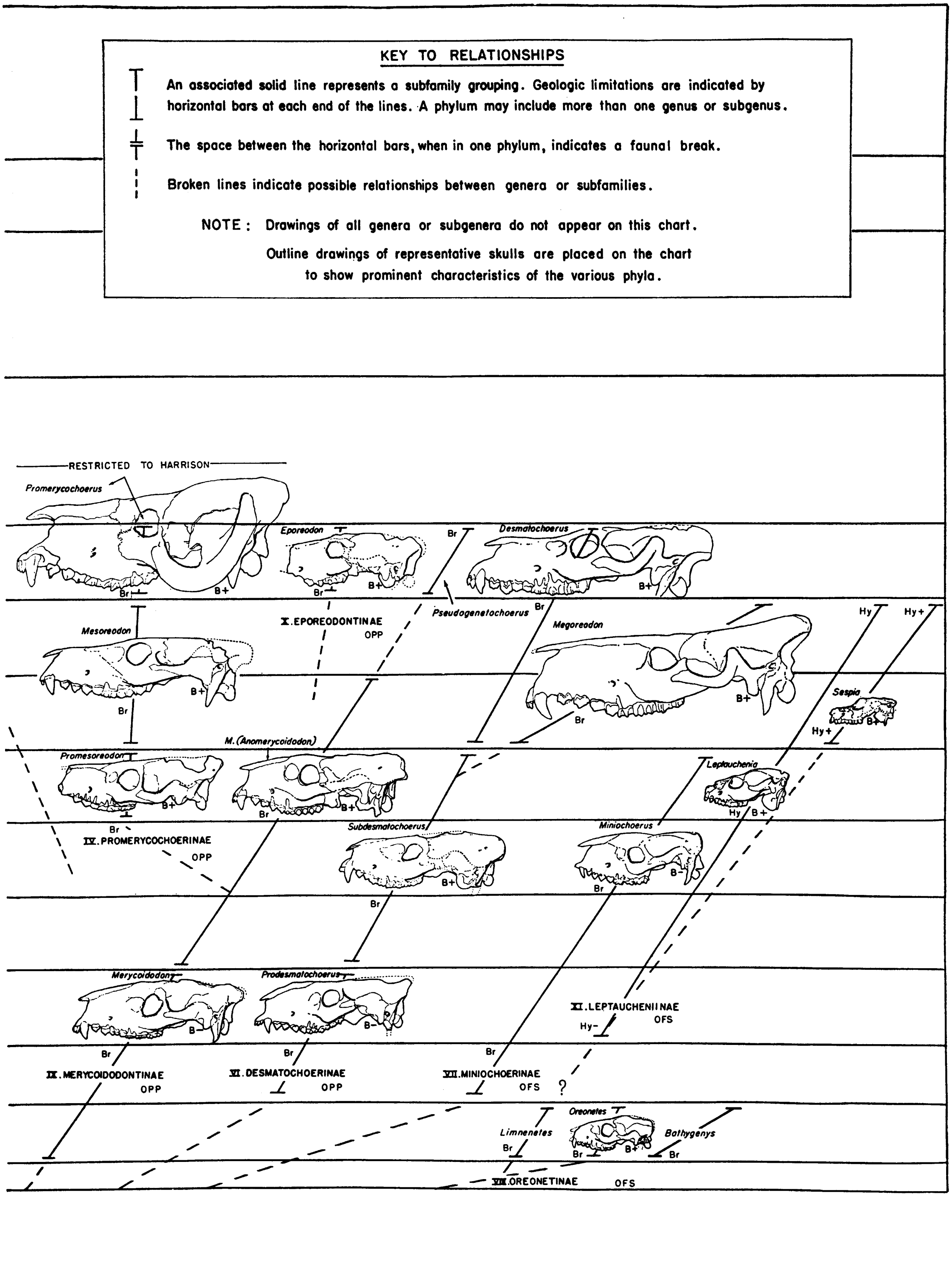


Chart 14 (on This Page and Opposite Page). Stratigraphic distribution of the 11 subfamilies of the Merycoidodontidae. (See p. 415.)


KEY TO RELATIONSHIPS
An associated solid line represents a subfamily grouping. Geologic limitations are indicated by horizontal bars at each end of the lines. A phylum may include more than one genus or subgenus.
The space between the horizontal bars, when in one phylum, indicates a faunal break.
Broken lines indicate possible relationships between genera or subfamilies.
NOTE: Drawings of all genera or subgenera do not appear on this chart.
Outline drawings of representative skulls are placed on the chart to show prominent characteristics of the various phyla.
RESTRICTED TO HARRISON
Promerycochoerus
Br
B+
Eporeodon
Br
B+
Br
Desmatochoerus
B+
X. EPOREODONTINAE
OPP
Pseudogenetochoerus
Br
Megoreodon
Hy
Hy+
Mesoreodon
B+
Br
Sespia
B+
Hy+
Br
M. (Anomerycoidodon)
Promesoreodon
B+
Br
B+
Leptauchenia
Hy
B+
Br
IV. PROMERYCOCHOERINAE
OPP
Subdesmatochoerus
B+
Br
Miniochoerus
B-
Br
Merycoidodon
B-
Prodesmatochoerus
B-
XI. LEPTAUCHENIINAE
OFS
Hy-
Br
Br
Br
IX. MERYCOIDODONTINAE
OPP
VI. DESMATOCHOERINAE
OPP
VII. MINIOCHOERINAE
OFS
?
Oreonetes
Limnenetes
Bathygenys
Br
Br
B+
Br
VIII. OREONETINAE
OFS

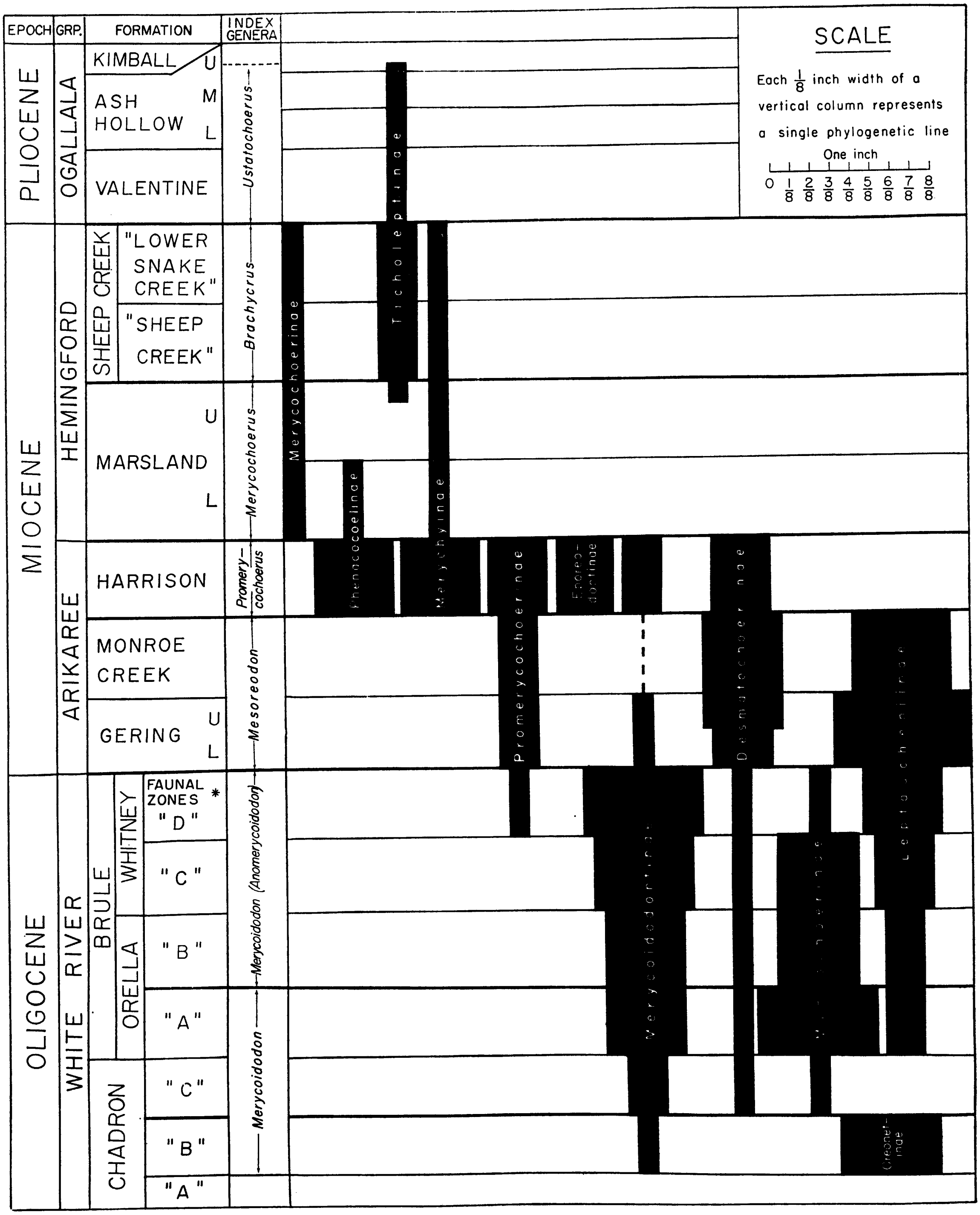


CHART 15. Stratigraphic distribution of the Merycoidodontidae, stressing the number of individual phylogenetic lines. (See p. 415.)

of the genera and subgenera, as well as the subfamily distribution. The X on a geological division line marks a hiatus in time. Compare chart 16 with chart 15.

All correlations throughout this revision are based on the central Great Plains geologic section (see chart 13, p. 411). The formational or member names from outside the central Great Plains have been considered, but have been omitted from all charts. This does not imply that the writers consider that the formational names used in the central Great Plains should be applied to deposits in Montana, Oregon, California, New Mexico, or other states not adjacent to the central Great Plains. The possibilities of correlation of deposits is far greater within the Nebraska panhandle area where the Oligocene, Miocene, and Pliocene deposits are so well exposed. In fact the stratigraphic sequence of continental deposits representing this portion of the geologic column is more complete than in any other region in North America. The formations in western Nebraska can readily be correlated with many localities in the adjacent states of South Dakota, Wyoming, and Colorado.

Some of the areas are controversial as to the geological ages of the fossils, chiefly because in each of these particular areas more than one formation (or member) is involved. In many instances collections from these localities contain mixed faunas. The faunas are mixed due to the fact that the collections were not made from a stratigraphic approach. The same is also true in some quarry assemblages. In some cases later channel deposits have been cut into older channel sediments, and it has been difficult to distinguish the unconformities. In other localities the unconformities have been obscured with talus covering or vegetation. The writers have tried to visit as many of these questionable localities as possible, in order to look for clues that might clarify the stratigraphic positions of the oreodont specimens involved.

In the Ricardo area of California and in the Santa Fe region of New Mexico the oreodonts (*Ustatochoerus*) appear to have survived somewhat later than in the central Great Plains, but even in these two localities the oreodonts appear to have become extinct before the deposition of the Kimball sediments in the Great Plains.

EXPLANATION OF CHART 17

Chart 17 is a map of the western United States, showing all general areas that have yielded oreodont remains. The states of Arizona, Oklahoma, Utah, and Washington lack oreodont remains to date, so far as known. A set of geologic symbols is applied to the various cited areas. Again, it should be noted that an area may include deposits of other ages than those cited. However, only those deposits from which oreodonts are known are here recorded.

The southeastern part of Wyoming, the southern part of South Dakota, and the complete Nebraska area are reproduced at a larger scale on page 424. This allows more detail in the close assemblage of local areas. Also a more detailed list of localities follows (see chart 17a).

EXPLANATION OF CHART 17A (SUPPLEMENT TO CHART 17)

The areas (F:A.M. and U.N.S.M. collecting localities) that are included in the over-all designations on chart 17 are as follows:

NEBRASKA

Banner County includes: Wild Cat Ridge area (continuation of Horse Creek Basin of Wyoming).

Dawes County includes: Horn, Brecht Ranch (or Brecht Dam), and Chadron areas, and all U.N.S.M. collecting localities with the symbol DW—.

Morrill County includes: Pumpkin Creek and Bridgeport areas, and all U.N.S.M. collecting localities with the symbol MO—.

Scotts Bluff County includes: Scotts Bluff Monument area, and all U.N.S.M. collecting localities with symbol SF—.

Sioux County includes: North of Harrison area, and all U.N.S.M. collecting localities with the symbol SX—.

SOUTH DAKOTA

Harding County includes: Slim Butte, Battle Mountain, and Point Creek areas.

Jackson County includes: Hodges Basin area.

Pennington County includes: Imlay, Scenic, Cain Creek, Miller Basin, and Saddle Horse Pass areas.

Shannon County includes: Sheep Mountain, Cottonwood Pass, Big Corral Draw, Little Cor-

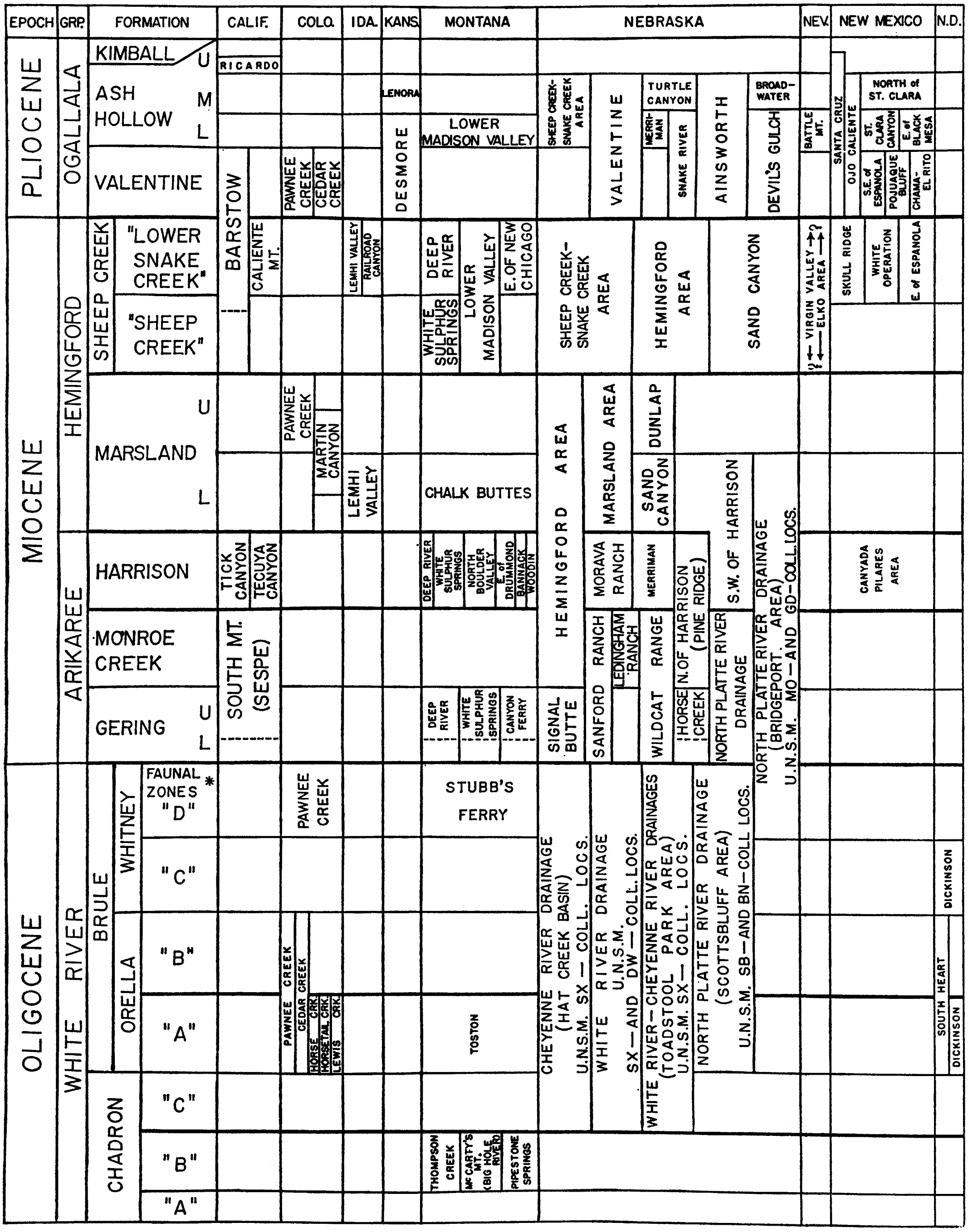
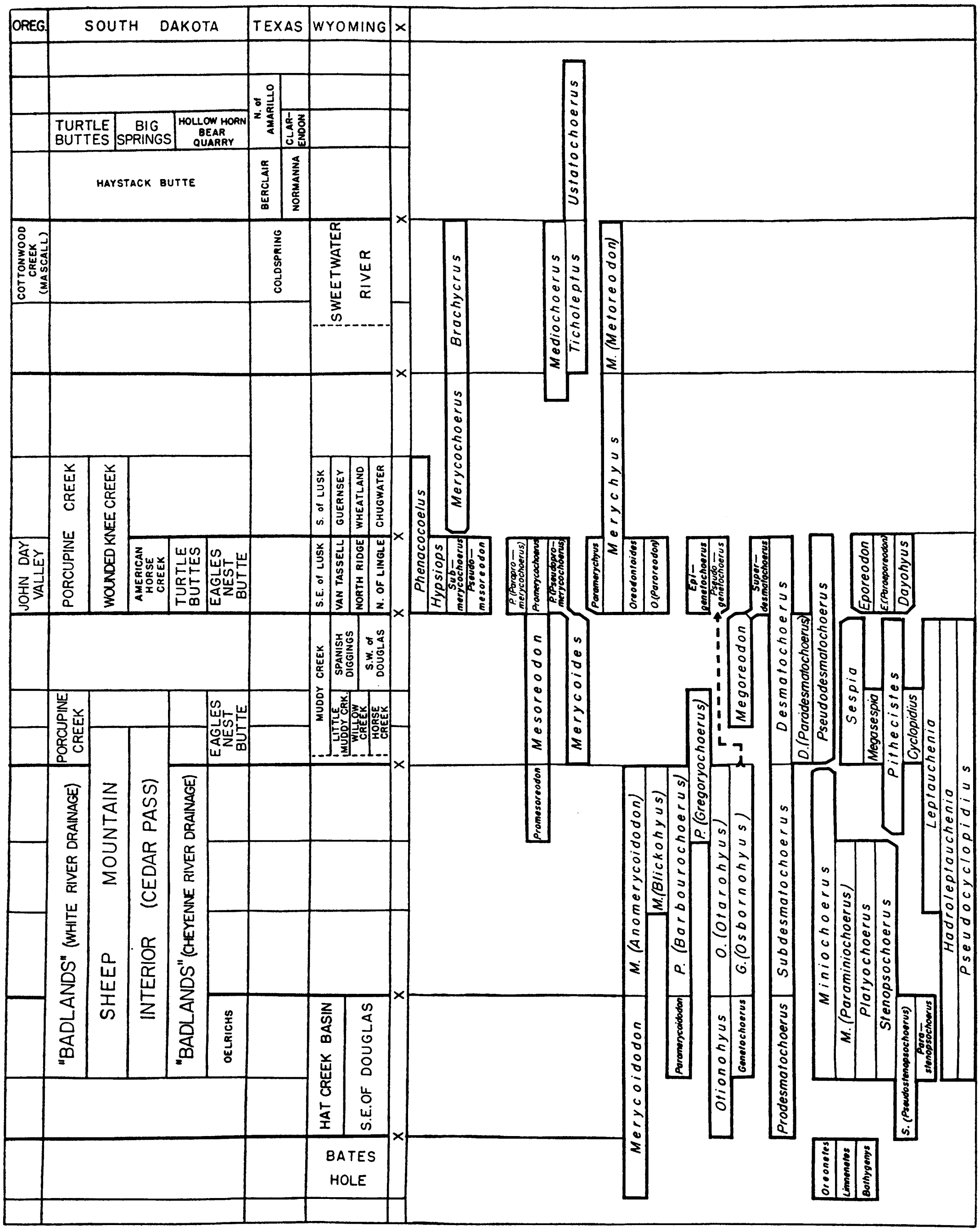


CHART 16 (ON THIS PAGE AND OPPOSITE PAGE). Proposed stratigraphic correlations of deposits in localities that have produced oreodont remains. (See p. 415.)


OREG.
SOUTH DAKOTA
TEXAS
WYOMING
TURTLE BUTTES
BIG SPRINGS
HOLLOW HORN BEAR QUARRY
N. of AMARILLO
CLARENDON
HAYSTACK BUTTE
BERCLAIR
NORMANNA
COTTONWOOD CREEK (MASCALL)
COLDSPRING
SWEETWATER RIVER
JOHN DAY VALLEY
PORCUPINE CREEK
WOUNDED KNEE CREEK
AMERICAN HORSE CREEK
TURTLE BUTTES
EAGLES NEST BUTTE
S. of LUSK
GUERNSEY
WHEATLAND
CHUGWATER
S.E. of LUSK
VAN TASSELL
NORTH RIDGE
N. OF LINGLE
MUDDY CREEK
SPANISH DIGGINGS
S.W. of DOUGLAS
LITTLE MUDDY CRK
WILLOW CREEK
HORSE CREEK
"BADLANDS" (WHITE RIVER DRAINAGE)
SHEEP MOUNTAIN
INTERIOR (CEDAR PASS)
"BADLANDS" (CHEYENNE RIVER DRAINAGE)
OELRICHS
HAT CREEK BASIN
S.E. OF DOUGLAS
BATES HOLE
Ustatochoerus
Brachycrus
Mediochoerus
Ticholeptus
M. (Metoreodon)
Merycochoerus
Merychyus
Phenacocoelus
Hypsiops
Sub-merycochoerus
Pseudo-mesoreodon
P. (Paraprо-merycochoerus)
Promerycochoerus
P. (Pseudopro-merycochoerus)
Paramerychyus
Oreodontoides
O. (Paroreodon)
Epi-genetochoerus
Pseudo-genetochoerus
Super-desmatochoerus
Desmatochoerus
D. (Paradesmatochoerus)
Pseudodesmatochoerus
Eporeodon
E. (Paroreodon)
Dayohyus
Mesoreodon
Merycoides
Megoreodon
Sespia
Megasespia
Pithecistes
Cyclopidius
Leptauchenia
Promesoreodon
P. (Gregoryochoerus)
Merycoidodon
M. (Anomerycoidodon)
M. (Blickohyus)
P. (Barbourochoerus)
Paramerycoidodon
Otionohyus
O. (Otarohyus)
G. (Osbornohyus)
Genetochoerus
Prodesmatochoerus
Subdesmatochoerus
Miniochoerus
M. (Paraminiochoerus)
Platyochoerus
Stenopsochoerus
S. (Pseudostenopsochoerus)
Parastenopsochoerus
Hadroleptauchenia
Pseudocyclopidius
Oreonetes
Limnenetes
Bathygenys

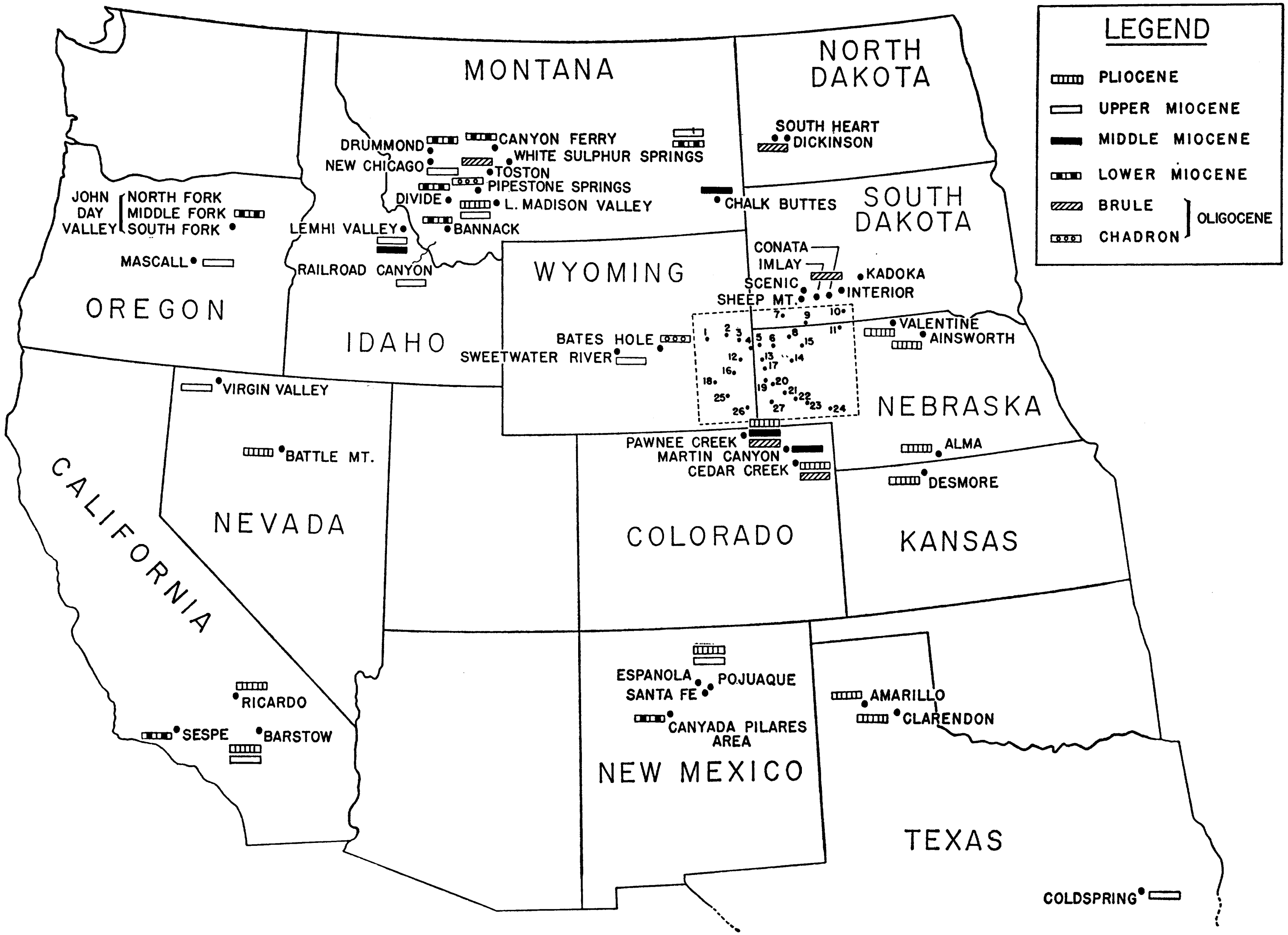


Chart 17. Geographic and geologic distribution of the oreodonts. (See chart 17a for more detailed locations and geology of localities 1–24 in Wyoming, Nebraska, and South Dakota.)

ral Draw, Battle Creek Draw, Battle Creek Canyon, and Quinn Draw areas.

Wyoming

The region south of Lusk includes: Royal Valley, 9 Mi. south of Lusk, Sand Gulch, 12–18 Mi. District, 25 Mi. District, Jay Em District, and Raw Hide Creek areas.

North Ridge includes: North of Lusk, North of Van Tassel, North of Node, North of Manville, and North of Keeline.

Horse Creek Basin includes: Goshen Hole, Bear Mountain, 66 Mountain, and Tremain areas. (66 Mountain is actually the west end of Wild Cat Ridge [or Range], Banner County, Nebraska.)

Hat Creek Basin includes: Seamen Hills, North of Node, Indian Creek, Shack Draw, and Spring Draw areas.

Additional Data

Because the number of amateur collectors and "rock hounds" has increased during the past 30 years, the exact position of various collecting localities has been omitted from the reports on the revision of the oreodonts. Amateurs frequently use published scientific papers as a source of information for adding to their private collections, and many of these amateurs collect and destroy valuable paleontologic material. Some amateur collectors, of course, preserve specimens in a scientific manner and do a commendable job in keeping records of the stratigraphic data connected with the fossils.

If more precise geographic or geologic data are needed by professional research workers for specific specimens mentioned in these papers on the revision of the Merycoidodontidae, the information can be obtained from the registrars of the Frick Laboratory at the American Museum of Natural History and the University of Nebraska State Museum.

EXPLANATION OF CHART 17B

Chart 17b represents a proposed correlation of middle and upper Oligocene and basal Miocene deposits in the Nebraska-Wyoming-South Dakota region. The various terminologies of formations, members, and faunal zones used by workers in the region are tentatively correlated for use in the interpretation of the stratigraphic distribution of the oreodont specimens listed in the present report. The boxes enclosing the geologic and faunal terms do not portray exact geologic time equivalents or lithic thicknesses.

The following notes refer to the letters *a* through *g* on chart 17B:

a Since 1907 various workers (Osborn, Wanless, Bump, and others) have considered the basal Arikaree White Ash (= Rockyford Ash) as Miocene, and have not included it in the Brule Formation. In 1956 Bump described two new geographic members of the Brule, the Scenic and the Poleslide, in South Dakota, which equate, at least in part, with the Orella and Whitney members of the Brule Formation in Nebraska.

b Morris F. Skinner followed the terminology in the published sections of Darton (1903a) as a basis for his collecting records. The present writers, however, consider that, in some localities, such as at Redington Gap in Morrill County and Castle Rock in Scotts Bluff County, Darton erroneously correlated portions of the Gering Formation with the upper part of the Brule. The Gering sediments in these and other localities seem to represent distant flood-plain facies and contain a large quantity of reworked Brule silt and clay, thus somewhat resembling the typical Brule of the region. The oreodont remains from these flood-plain sediments appear to be similar to those attributed to the Gering and are quite distinct from those derived from the upper Brule (see p. 402) for further discussion of this problem).

c Prior to the naming of the Sharps Formation by Harksen, Macdonald, and Sevon (1961), Skinner related the various specimens collected in South Dakota (1938–1962) to the First White Layer (= Rockyford Ash) which occurs at the base of the Sharps in the Sheep Mountain area.

d Prior to the naming of the Rockyford Ash by Nicknish and Macdonald in 1963, Skinner and his associates used the term "First White Layer" for this volcanic ash layer. Nicknish originally proposed the term "Rockyford Ash" in 1957 in an unpublished master's thesis (South Dakota School of Mines and Technology), but a published description did not appear until 1963.

e These letters indicate divisions of the Whitney and Orella members of the Brule Formation designated by Schultz and Stout as guides

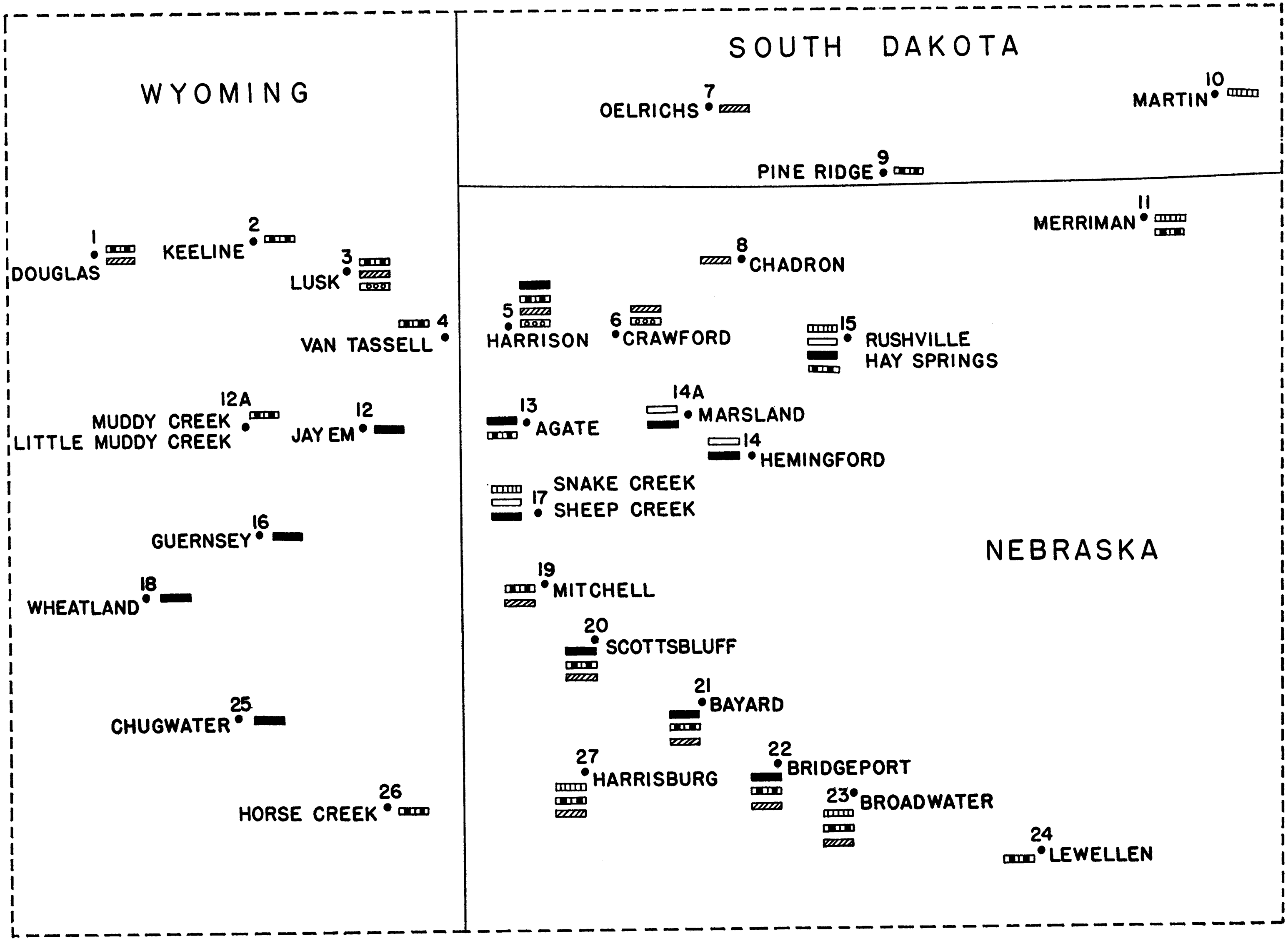


CHART 17A. Chief oreodont collecting localities in southeastern Wyoming, northwestern Nebraska, and southwestern South Dakota. (See chart 17 for legend pertaining to the geology of the various localities.)

NEBRASKA-WYOMING						SOUTH DAKOTA			
Formations named by Darton (1898, 1899a)	Members of Brule Formation named by Schultz and Stout (1938)	Divisions of Orella and Whitney; Schultz and Stout (1955)	Divisions of Orella and Whitney; Schultz, Tanner, Harvey (1955)	Oreodont faunal-zone terminology; Schultz and Falkenbach (1951, 1954, 1956, 1961)	Terminology of Skinner in Nebraska in collecting F:A.M. oreodonts, 1942-1962	Terminology of Skinner and associates in South Dakota in collecting F:A.M. oreodonts, 1938-1962	Oreodont faunal-zone terminology; Schultz and Falkenbach (1951, 1954, 1956, 1961)	Terminology of Wanless in geologic studies in South Dakota (1923)	Terminology of J. D. Bump in geologic studies in South Dakota (1956)[a]
Gering Formation				Gering	Gering of Darton[b]	Leptauchenia beds: Sharps Formation[c]	Gering equivalent	Rosebud beds	Arikaree
Volcanic ash in base of lower member						Leptauchenia beds: FIRST WHITE LAYER[d] =Rockyford Ash		White Ash Layer	Basal Arikaree White Ash
Brule Formation: Volcanic ash	Whitney Member	C[e] UPPER ASH	Upper Whitney UPPER ASH	Oreodont Faunal "Zone D" of Brule Formation	Whitney Member: Upper Whitney Second or Upper Ash	Leptauchenia beds: Lower Leptauchenia beds[f]	Oreodont Faunal "Zone D" of Brule Formation	Leptauchenia	Brule Formation, Poleslide Member: Upper Poleslide
Brule Formation	Whitney Member	B	Middle Whitney	Oreodont Faunal "Zone D" of Brule Formation	Whitney Member: Middle Whitney First or Lower Ash	Leptauchenia beds: Lower Leptauchenia beds[f]	Oreodont Faunal "Zone D" of Brule Formation	Upper Oreodon	Poleslide Member: Middle Poleslide
Brule Formation: Volcanic ash	Whitney Member	LOWER ASH A	LOWER ASH[g] Lower Whitney	LOWER ASH Faunal "Zone C" of Brule Formation	Whitney Member: Lower Whitney	Upper Oreodon beds[f]	Faunal "Zone C" of Brule Formation	Middle Oreodon	Poleslide Member: Lower Poleslide
Brule Formation	Orella Member	D	Upper Orella	Faunal "Zone B" of Brule Formation	Orella Member: Orella	Upper Nodules (at top) Middle Oreodon beds[f]	Faunal "Zone B" of Brule Formation	Lower Oreodon	Scenic Member: Upper Scenic
Brule Formation	Orella Member	C	Middle Orella	Faunal "Zone A" of Brule Formation	Orella Member: Orella	Lower Oreodon beds[f] =Lower Nodules	Faunal "Zone A" of Brule Formation	Lower Oreodon	Scenic Member: Lower Scenic
Brule Formation	Orella Member	B	Lower Orella	Faunal "Zone A" of Brule Formation	Orella Member: Orella	Lower Oreodon beds[f] =Lower Nodules	Faunal "Zone A" of Brule Formation	Lower Oreodon	Scenic Member: Lower Scenic
Brule Formation	Orella Member	A	Lower Orella	Faunal "Zone A" of Brule Formation	Orella Member: Orella	Lower Oreodon beds[f] =Lower Nodules	Faunal "Zone A" of Brule Formation	Lower Oreodon	Scenic Member: Lower Scenic

CHART 17B. Proposed correlation of middle and upper Oligocene and basal Miocene deposits in the Nebraska-Wyoming-South Dakota region.

for the stratigraphic collecting of mammals in the Oligocene deposits of Nebraska and adjacent areas.

f The faunal names for the beds of the Brule Formation in South Dakota were used as lithic units by Skinner and his associates in connection with the collecting of oreodont evidence (1938–1962). Skinner used the idealized geologic section of Osborn (1907a, p. 239, fig. 2) as the basis for his stratigraphic divisions, and Bump formalized the faunal names in South Dakota in 1956 when he substituted lithic names for the faunal units. However, Skinner's field data correspond to the lithic names proposed by Bump (1956).

g It should be noted that the Lower Ash is included in the Lower Whitney (= Whitney A), but the faunal break is actually at the base of the ash deposit. The ash is involved in a paleosol complex at many localities, which makes the matter of a lithic break difficult to determine. Although Schultz and Stout, and Schultz, Tanner, and Harvey have considered the Lower Ash of the Whitney Member of the Brule Formation as the uppermost part of the Lower Whitney, the faunal break as well as the chief lithologic break appears to be at the base of the Lower Ash. Morris F. Skinner includes his First or Lower Ash in the Middle Whitney. The oreodont remains from the Lower Ash are typical of the Middle Whitney examples and appear to differ from those of the Lower Whitney. The present writers have included the oreodont specimens from the Lower Ash in the oreodont faunal "Zone D" of the Brule Formation. The chart by Falkenbach and Schultz (1951) did not indicate this zonation, but the present paper gives the first oreodont faunal evidence from the Lower Ash. Therefore the oreodont evidence is included in faunal "Zone D" of the Brule.

EXPLANATION OF CHART 18

Chart 18 shows graphically the development of the skulls of *Merycochoerus* and *Brachycrus* during the medial and late Miocene. The genus *Merycochoerus,* although having a limited geologic range, is one of the outstanding examples of rapid phylogenetic development. Examples of *Merycochoerus* have been recorded only from the Marsland Formation. Noticeable morphologic differences are found in the skulls from the lower, middle, and upper Marsland Formation. The rate of change of certain morphologic characters was very rapid during medial Miocene times.

The genus *Brachycrus,* which was derived from *Merycochoerus,* also evolved at a fairly rapid rate during the late Miocene. The phylogenetic line was terminated at the end of the Miocene when the oreodonts belonging to the genus *Brachycrus* became extinct. It will be noted that in the development of *Brachycrus* the skulls became smaller, although the nasals continued to retreat; also the premaxillae became shorter. Both trends are the reverse of those shown in *Merycochoerus,* the ancestral genus.

The most obvious osteological changes that occurred in *Merycochoerus* are as follows:

a. There was a considerable change in the lengths of the anterior borders of the premaxillae. The premaxillae of *M. proprius* from the upper Marsland are from three to four times as long as those of *M. matthewi* from the lower Marsland. There is a gradual gradation in the sizes of the premaxillae of *Merycochoerus* from the lower to the upper parts of the Marsland Formation.

b. There was a progressive posterior retraction of the anterior border of the nasals of *Merycochoerus* during medial Miocene times. The comparative lengths of the nasals of examples of *Merycochoerus* from the lower Marsland were considerably greater than those from the upper Marsland. The height of the facial region below the nasals and above the tooth row also is noticeably higher in upper Marsland forms.

c. The infraorbital foramina are in the area above P^4–M^1 in the two species and one subspecies of *Merycochoerus.* The orbits, however, migrated from the region above the anterior part of M^3 (in early Marsland time) to the area above the posterior portion of M^3 (by late Marsland time).

d. The position of the external auditory meatus differs between the forms of the lower and those of the upper Marsland. The external auditory meatus of *M. matthewi* from the lower Marsland is comparatively high on the side of the skull in contrast to the decidedly lower position noted in *M. proprius* from the upper Marsland. The external auditory meatus of the middle Marsland subspecies has an intermediate position.

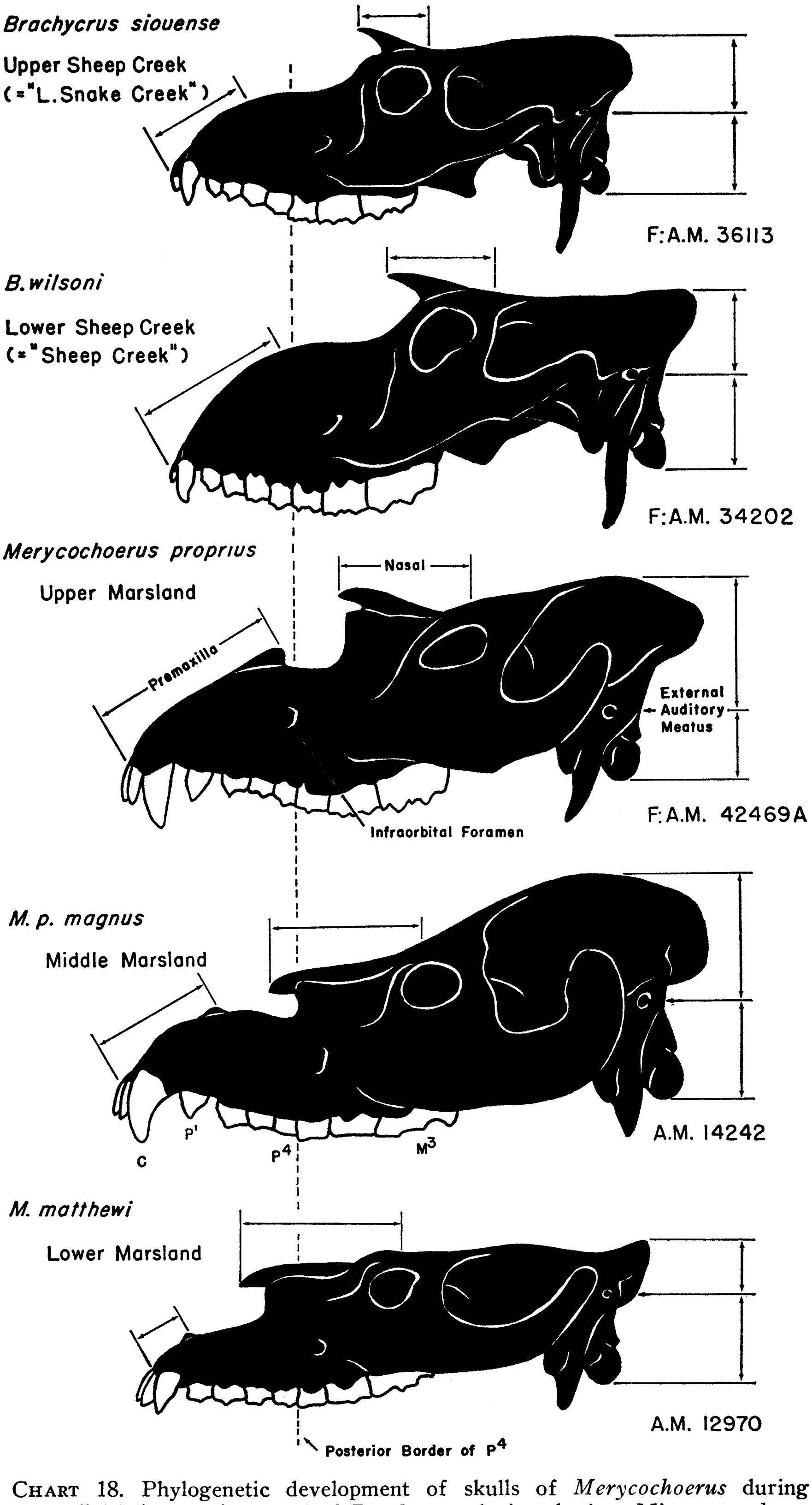


CHART 18. Phylogenetic development of skulls of *Merycochoerus* during medial Miocene times and of *Brachycrus* during the late Miocene. $\times\frac{1}{4}$.

e. The cheek teeth, especially the molars, had a tendency to have higher crowns in upper Marsland examples of *Merycochoerus*, but they were still brachyodont.

The most obvious osteological changes that occurred in *Brachycrus* are as follows:

a. There was a noticeable shortening of the lengths of the anterior borders of the premaxillae. The premaxillae of *B. wilsoni* from the lower Sheep Creek are shorter than those of *M. proprius* from the upper Marsland. This is a reversal of the trend that started during the medial Miocene when there was a gradual increase in the lengths of the premaxillae in the entire *Merycochoerus* line. The premaxillae of *B. siouense* from the upper Sheep Creek is even more abbreviated than those of *B. wilsoni* from the lower Sheep Creek. Hence the shortening of the anterior borders of the premaxillae apparently continued until *Brachycrus* became extinct.

b. A progressive posterior retraction of the anterior border of the nasals of *Brachycrus* continued during the late Miocene. This trend, of course, is noted in *Merycochoerus*, the ancestral form. The trend for the shortening of the nasals continued throughout the late Miocene. This trend also was noted in *Merycochoerus*.

The shortening as well as retraction of the nasals in the *Merycochoerus-Brachycrus* line appears to give additional evidence that these oreodonts gradually evolved from typical plains forms to river valley and forest animals during medial and late Miocene times. In the lower Marsland deposits (early medial Miocene) the fossilized remains of *Merycochoerus* are found chiefly in distal flood-plain deposits, and in the upper Sheep Creek (= "Lower Snake Creek") sediments (late Miocene) the bones of *Brachycrus* are found in stream-channel deposits. The morphology of the skull indicates that *Brachycrus* had a proboscis similar to that of the modern tapir. Scott[1] illustrated a splendid restoration of the head of an oreodont of this genus from the upper Miocene, showing a well-developed proboscis.

c. The position of the infraorbital foramina migrated posteriorly to the area above M^1–M^2 during the time *Merycochoerus* evolved to *Brachycrus*. In *Merycochoerus* the infraorbital foramina are above P^4–M^1. There is a definite "faunal break" between *M. proprius* and *B. wilsoni* (see p. 409, this paper, for further discussion). The orbits of *B. wilsoni* are similar in position to those of *M. proprius*, i.e., above the posterior of M^3, although in *B. siouense* from the upper Sheep Creek there apparently was a slight tendency for a forward migration of the orbit.

[1] 1913, fig. 198.

d. The position of the external auditory meatus of *Brachycrus* is about halfway between the top of the sagittal crest and the bottom of the occipital condyles. This is more like the intermediate position which is noted in middle Marsland examples of *Merycochoerus*.

e. The molars of *Brachycrus* certainly have much higher crowns than those of *Merycochoerus* and must be considered to be hypsodont.

EXPLANATION OF CHART 18A

The changes in certain morphologic characters in the skulls of the phylogenetic line of *Merychyus-Ticholeptus-Ustatochoerus* took place comparatively slowly. This was a conservative, slowly evolving line in contrast to the rapidly changing *Merycochoerus-Brachycrus* line. The most rapid development in the former line took place during medial Pliocene times shortly before extinction of the group. All species are recorded from geologic formations of the western Nebraska region. *Merychyus* is from the Harrison Formation (lower Miocene); *M. arenarum*, from the Marsland (middle Miocene); *Ticholeptus hypsodus*, from the Sheep Creek (upper Miocene); *Ustatochoerus medius*, from the Valentine (lower Pliocene); *U. profectus*, from the lower part of the Ash Hollow (lower portion of middle Miocene deposits); and *U. major*, from the middle part of the Ash Hollow (middle portion of middle Pliocene deposits).

The most obvious osteological changes that occurred in the *Merychyus-Ticholeptus-Ustatochoerus* line are as follows:

a. There was a slight but gradual retraction of the nasals during the Miocene. This process was speeded up rapidly during early and medial Pliocene times.

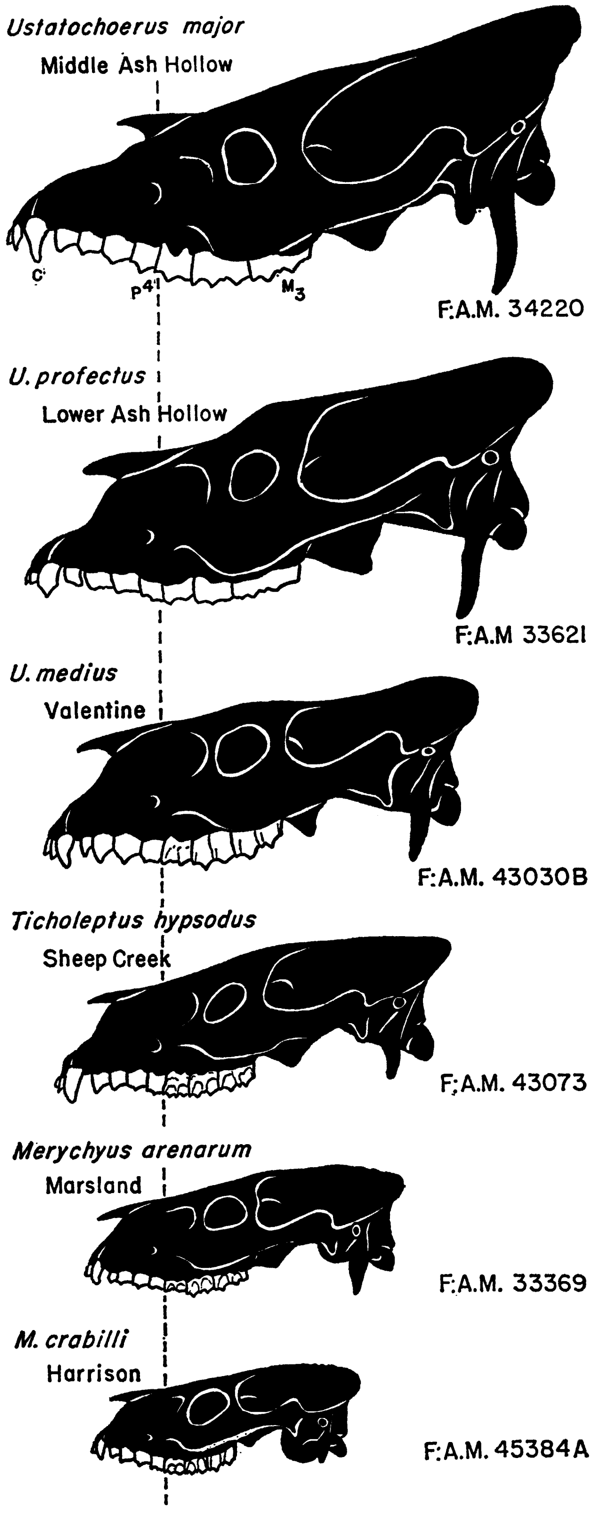


CHART 18A. Phylogenetic development of skulls of the *Merychyus-Ticholeptus-Ustatochoerus* line from early Miocene to medial Pliocene times. $\times\frac{1}{4}$.

b. The early and medial Miocene forms had low, comparatively flat skulls. From late Miocene to medial Pliocene times the supraoccipital region of the skull became increasingly elevated.

c. The cheek teeth were brachyodont during the early Miocene but became increasingly hypsodont until the time of extinction in medial Pliocene times, when the molars had reached a moderately hypsodont stage of development.

EXPLANATION OF CHART 19

The graphic comparison of the skulls of the six phylogenetic lines of leptauchenins demonstrates how "splitting" of lines can occur when precise stratigraphic data are available for all the specimens involved. The proposed phyla are based on morphologic characters combined with the stratigraphic information.

One character, the large orbits, effectively separates the skulls of the tribe Sespiini from those of the Leptauchiini. The very hypsodont molars with the very weak external styles of the Sespiini, of course, do not show on the drawings, but were considered along with other characters when the present writers did the "splitting" of the lines.

Thorpe had a strong tendency to "lump," which may have been necessary because he lacked sufficient stratigraphic evidence to do otherwise. Thorpe (oral communication) frequently encouraged the writers to concentrate on obtaining all the stratigraphic data possible before attempting a revision of the oreodonts. He pointed out the handicaps that confronted him when he tried to do taxonomic work with the oreodonts without sufficient geological information.

A typical example of what can happen in a revision when the stratigraphic data are not available or considered is to be found in Thorpe's monograph[1] on "The Merycoidodontidae." Chart 19 of the present paper will help the reader to visualize the complexity and implications. Thorpe did not illustrate or consider the original type material (A.N.S.P. 10878, and others) of *Leptauchenia decora* Leidy from the upper Brule (9 on chart), perhaps because it was too fragmentary, but did use an immature example (A.N.S.P. 10940) of *Pseudocyclopidius major* Leidy from the lower Gering (19 on chart) for a "genocotype" of *L. decora.* He also used a mature skull and mandible (the holotype, U.N.S.M. 28408) of *Megasespia middleswarti* Schultz and Falkenbach from the upper Gering (4 on chart) for a "plesiotype" of *L. decora.* Superficially, the three specimens resemble one another, but they come from deposits of three different geologic ages, and actually the morphologic characters show that the specimens represent three distinct phylogenetic lines. Thorpe ran into further complications in considering the species *L. decora,* when he did not compare Leidy's original type material with that of his own holotype (Y.P.M. 10123) of "*Cyclopidius* (*Chelonocephalus*) *schucherti* Thorpe," probably because the Yale Peabody Museum holotype did not have the correct geologic data associated with it, since Thorpe recorded it as coming from the "Sheep Creek, Middle Miocene" (upper Miocene of the present writers) deposits from "near Hermosa, South Dakota." The specimen undoubtedly came from the upper Brule from near Hermosa. There are no known deposits of Sheep Creek age in the vicinity, but there are numerous exposures of upper Brule (Whitney Member) sediments. Thorpe's holotype of "*C.* (*Chelonocephalus schucherti*" is typical of the many examples of *Leptauchenia decora* from the "*Leptauchenia* beds" (middle and upper Whitney) of the South Dakota Oligocene badlands, and the dentition is similar in size and form to that of Leidy's type (A.N.S.P. 10878). Hence, it is evident that Thorpe "lumped" the characters of two distinct phylogenetic lines in the Leptauchenini with those of one line in the Sespiini when he considered the characters of *L. decora.*

Thorpe[2] also "lumped" *Sespia californicus* (Stock) [approximately same as 2 on chart 19], *Hadroleptauchenia densa* (Loomis) [16 on chart], *Pseudocyclopidius lullianus* (Thorpe) [20 on chart], and *Cyclopidius simus* Cope [13 on chart] under the genus *Cyclopidius,* apparently without evaluating the critical osteological characters. All these were contemporaneous species, living at about the same time. Many workers have considered the genera and species of oreodonts on a "horizontal" or "lateral" basis, rather than on a "perpendicular" or "geo-

[1] 1937, pp. 235, 256, 380, pl. 35, figs. 1-5.

[2] 1937, p. 242.

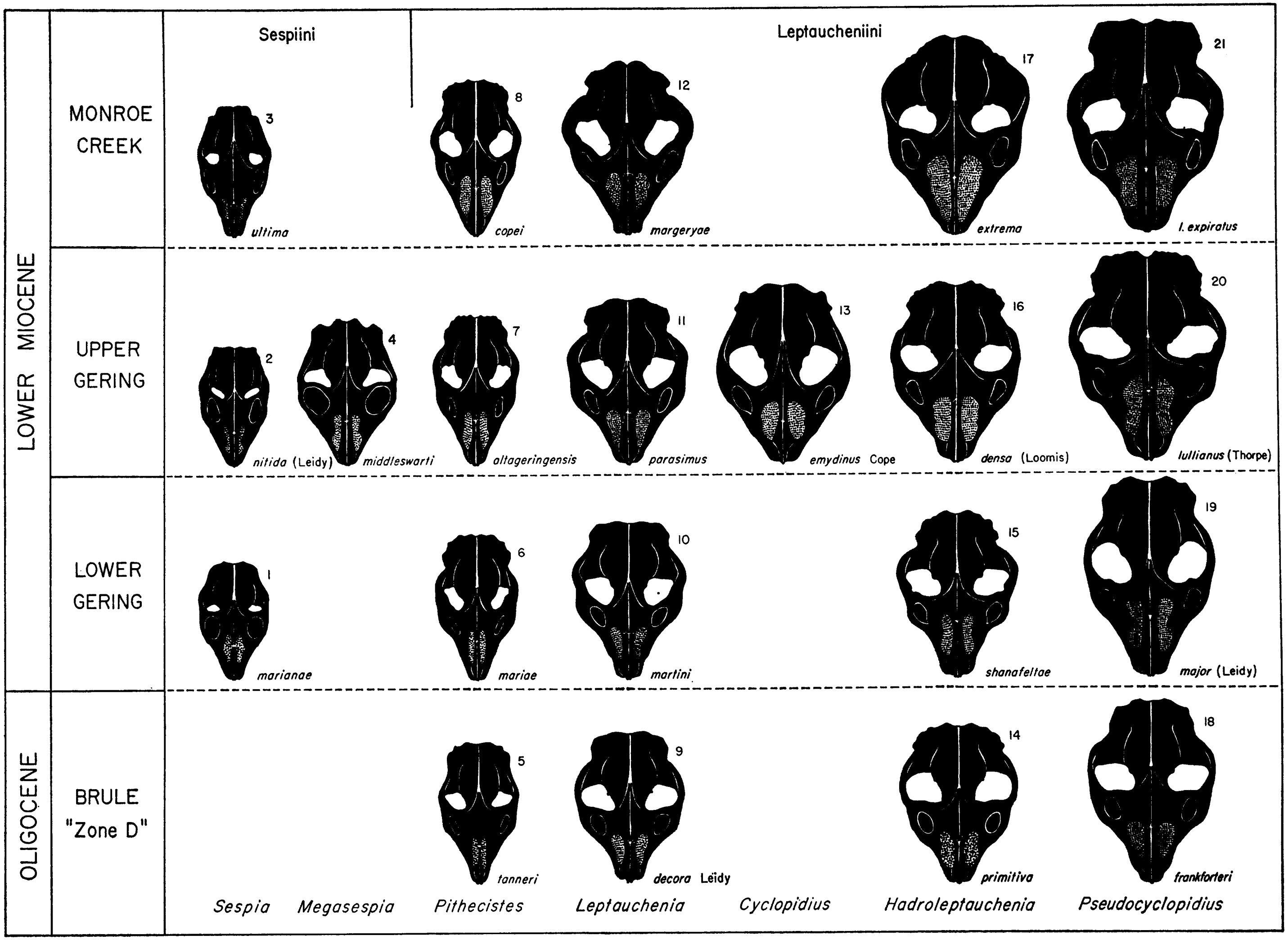


CHART 19. Comparison of skulls in the six phylogenetic lines of the Leptaucheniinae. Skulls are typical of examples in the F:A.M. and U.N.S.M. collections, with restorations based on available evidence. $\times\frac{1}{5}$.

logic" basis with primitive forms giving rise to more specialized ones (see discussion on primitive and specialized, this paper, p. 458). The "horizontal" or "lateral" approach always encourages "lumping," which in turn induces erroneous conclusions.

The three genera *Pseudocyclopidius, Hadroleptauchenia,* and *Leptauchenia* should be compared for a better understanding of the parallel development that took place during late Oligocene and early Miocene times in these phylogenetic lines. It might be said that the *Pseudocyclopidius* line was the most progressive and the *Leptauchenia* line was the least progressive. Therefore, it might be easy to jump lines in the identification of specimens. *Pseudocyclopidius frankforteri* (18 on chart) was far more specialized in the late Oligocene than either *H. primitiva* (14) or *L. decora* (9), which were contemporaneous species. It might be easy to consider *H. shanafeltae* (15) from the early Miocene (lower Gering) as perhaps the same species as *P. frankforteri* (18 on chart) from the late Oligocene (upper Brule), if the "horizontal" or "lateral" approach of taxonomy were used. Also *L. parasimus* (11) from the lower Miocene (upper Gering) was at about the same stage of evolution but in a separate phylum as *P. frankforteri* (18) in the late Oligocene. Thus these two species in separate phylogenetic lines might be considered as the same, if the "horizontal" approach were used.

When the leptauchenins were first considered for revision, typical skulls and jaws of all known forms were placed on a large, stratigraphically marked table according to the geologic occurrence of each specimen. Then those of similar characters from the different formations were sought, and eventually tentative lines were established. At first there was a tendency to "lump," but as more specimens became available and more precise geologic data were considered, the lines could sometimes be "split" into two or more other lines. At first the present writers considered only three lines of leptauchenins: (1) *Sespia,* including *Megasespia;* (2) *Leptauchenia,* including *Pithecistes* and *Cyclopidius;* and (3) *Pseudocyclopidius,* including *Hadroleptauchenia.* As the research work progressed, it became evident that there was too much "lumping" of critical characters. Chart 19 as presented, therefore, represents the arrangement of the phylogeny table after all the shifting of material was completed. This approach was used throughout the oreodont revision.

CHARACTERS, TAXONOMY, AND VARIATION IN THE MERYCOIDODONTIDAE

ORDER ARTIODACTYLA OWEN

Artiodactyla OWEN, 1848, p. 131.

INFRAORDER OREODONTA OSBORN

Oreodonta OSBORN, 1910, p. 549.

SUPERFAMILY **MERYCOIDODONTOIDEA** THORPE

Merycoidodontoidae THORPE, 1937, p. 23.

FAMILY **MERYCOIDODONTIDAE** THORPE

Merycoidodontidae THORPE, 1923c, p. 239.
Oreodontidae LEIDY, 1869, p. 71.
Cotylopidae LYDEKKER, 1896, p. 373.

CHARACTERS

SKULL: Very small to large in size (smallest examples, *Bathygenys alpha,* with a skull the size of a recent jack rabbit; largest forms, *Megoreodon grandis loomisi,* with skulls almost the size of a recent race horse, an apparent 479% difference in over-all length of the skulls of the two extremes); dolichocephalic to brachycephalic; low to high; sagittal crest from slight ridge to pronounced; supraoccipital wings varying from widely spread and incorporated into fan-shaped occipital region to those produced posteriorly beyond occipital condyles; frontals narrow to broad; lacrimal fossa small to large, shallow to deep; without or with facial, frontal, or occipital vacuities; nasals with no anterior reduction to those anteriorly shortened (to a point above anterior border of orbit); zygomatic arch light to robust, posterior border low to high; premaxillae from barely joined to considerable length of ossification; bulla minute to very inflated; postglenoid process light, robust, peg-shaped, or anteroposteriorly compressed, with external border straight to sloping downward and inward.

MANDIBLE: Inferior border of ramus straight to convex (as in *Brachycrus*); ramus shallow to deep, ascending ramus high to extremely high.

DENTITION: Brachyodont (as in Merycoidodontinae) to exceptionally hypsodont (as in *Sespia,* in which the M_2 and M_3 are comparatively more hypsodont than in the recent horse; see fig. 42); formula I^{2-3}_{3}, C/C, P^4_4, M^3_3, no loss of teeth except that one incisor may be absent from the leptauchenins, no noticeable diastema between C/C and P^1_1; /C incisiform; P_1 caniniform; P^1–P^4 each with or without weak to strong anterior intermediate crest; P^2–P^4 each with or without weak to strong posterior intermediate crest; external styles of molars from very weak to absent (in *Sespia*) to exceptionally pronounced (in *Merycochoerus*); inferior and superior fossettes shallow (in Miniochoerinae and Leptaucheniinae) to deep (in Desmatochoerinae); anterior and posterior crests from a marked degree of internal slope (in Oligocene forms) to a noticeably lesser degree (in forms later than Oligocene in age).

LIMBS: From short and light (in Miniochoerinae) to comparatively long and robust (in *Megoreodon*); five-toed manus in some Oligocene and lower Miocene forms; four-toed pes in all species.

DISCUSSION

The Merycoidodontidae remains indicate that there was a general tendency for the skulls to evolve from small to large in size (with the possible exception of those of *Brachycrus* from the "Sheep Creek"-"Lower Snake Creek" deposits of Sioux County, Nebraska; see detailed discussion, p. 409). Many changes and variations in the skulls are apparent in the foregoing list of characters. The combination of these characters differs in the various genera.

In examples of *Brachycrus, Merycochoerus,* and *Submerycochoerus,* the anterior nasal borders are retracted posteriorly. In the two former genera the premaxillae are joined for a considerable distance, whereas, in the latter genus, the nasal is not retracted nearly so far as in *Merycochoerus,* and the premaxillae are not joined for so great a distance (see chart 18a, p. 429, for indication of the change in the length of the premaxillae during the medial Miocene).

The dental formula remains essentially the same throughout the history of the family. The tooth series change from being light to very robust, or from brachyodont to hypsodont, but these changes are gradual within a phylogenetic line.

The deciduous dental formula was intentionally omitted from the dental characters above owing to a lack of definite conclusions on the part of the present writers (see following discussion).

Leidy[1] in his report on the "Oreodontidae" [= Merycoidodontidae], published the dental formula as: "Incisors $\frac{33}{44}$; c. $\frac{11}{11}$; p.m. $\frac{44}{33}$; m. $\frac{33}{33}$ = 44. Well-developed incisors in both jaws; the fourth of the lower jaw being a transformed canine, as in ordinary ruminants. Canines well-developed and strong in both jaws, suilline in their resemblance, those of the lower jaw being transformed premolars. The anterior three premolars having the crown in the form of a demi-cone, with more or less rudimental elements at the base internally. The fourth upper premolars and the true molars of both jaws constructed after the ordinary ruminant type, and most nearly resembling in form those of the Deer family."

Apparently Leidy considered the incisiform lower canine as an incisor, and the caniniform lower premolar one as the canine; hence his formula of four lower incisors and only three inferior premolars.

Leidy, on page 79 of his report, discussed the dentition of *Oreodon* [= *Merycoidodon*] and stated: "As previously intimated, the dentition of *Oreodon* is remarkable for its complete character," but the formula given is the same as the one he reported on page 71. He emphasized his conclusion that the lower dental series contained just three premolars by saying, "The molar teeth, seven in the upper jaw and six in the lower jaw on each side." Also, on page 82, Leidy wrote, "The lower premolars, three in number."

Leidy (p. 85) considered the deciduous dentition and concluded: "*Temporary dentition.*—The temporary dentition of *Oreodon* was probably arranged according to the following formula: In. $\frac{3-3}{4-4}$; c. $\frac{1-1}{1-1}$; p.m. $\frac{2-2}{2-2}$; m. $\frac{1-1}{1-1}$ = 30.

"Specimens under examination contain the temporary molar teeth and the upper canines, but no others.

"The upper temporary true molar [dP^4] has the same form as those of the permanent set, but is smaller.

"The crown of the upper second temporary premolar [dP^3] is composed of three lobes like those of the true molar; two behind and transverse, the other in front. It has the appearance of the fourth permanent premolar conjoined with an anterior premolar. The anterior lobe internally is connected with the adjacent part of the postero-internal lobe by means of festooned fold, enclosing between them a depression. . . .

"The first permanent premolar of the upper jaw protruded after the deciduous teeth behind, and appears not to have had a predecessor.

"The lower temporary true molar [dP_4], as in other ruminants, possesses three pairs of lobes, which hold the same relative position with one another and have the same form as the pairs of lobes in the permanent true molars."

In the permanent formula, Leidy recognized four superior premolars and three molars. However, in the temporary superior premolars he considered dP^4 as "dM^1" and dP^3 as "dP^2." Hence he gave his formula with two deciduous premolars.

O'Harra[2] published a paper on a unique block which contained a female example of *Merycoidodon culbertsonii* with unborn twins (S.D.S.M. 28129). The present writers have seen the group of three ("mother and foetal twins") but did not examine the specimens out of the exhibition case.

Under a discussion of *Merycoidodon culbertsonii,* Thorpe[3] discussed an immature skull and mandible under the number S.D.S.M. "311" (the correct number is 31133). Thorpe stated, "This skull belongs to one of the skeletons of a pair of foetal twins, found lying within the pelvic girdle of an excellently preserved skeleton of *M. culbertsonii.*"

From the illustrations published by Thorpe, it did not seem reasonable that one of the foetal twins could possess deciduous dentition, erupted to the degree illustrated. For clarification, the writers wrote to Morton Green and John Clark at the South Dakota School of Mines, and they kindly sent the specimen to the present writers for study. They also provided the following information[4]: "The specimen referred to, SDSM No. 311, is incorrectly cited in both Thorpe and Scott [1940] and should be corrected to SDSM No. 31133. The follow-

[1] 1869, pp. 71, 79, 82, 85.

[2] 1930.

[3] 1937, p. 55, pl. 2, figs. 3–4.

[4] Letter, February 20, 1961.

ing data is [*sic*] from the [SDSM] catalogue card. Collected about 1890 by Geo. E. Osterhaut and traded to SDSM for a dicerathere jaw. It [SDSM No. 31133] was found at Pawnee Buttes, 50 mi. E. by N. of Greeley, Colorado.

"The number for the twins is SDSM No. 28129. Lower *Oreodon* beds, Cain Creek, Pennington County, [South Dakota]."

It is interesting that Green said earlier in conversation with the present writers, "Number 31133 looks like a baby miniochoerin to me . . ." After the skull in question was received, it became apparent that the adolescent skull and mandible were referable to the Miniochoerinae. The fan-shaped occipital region of the adolescent skull is typical of that subfamily and not like the posteriorly projected occipital wings of the Merycoidodontinae. Thorpe considered the adolescent skull and mandible (S.D.S.M. 31133) referable to *Merycoidodon culbertsonii.*

Thorpe further stated: "Professor W. B. Scott very kindly gave me a photograph of this most interesting specimen, and Mr. Bruce Horsfall most generously made the illustrations, shown in Pl. II, figs. 3–4. . . . The lower incisors are much longer than the superior. The canines are like pegs. The true canine has the shape and size of the lower incisors, and all are nearly uniform in shape and especially in size. There are but three teeth behind the canine in both jaws." The present writers consider the lower canine decidedly larger than the lower incisors. A comparison of size may be seen in Thorpe's illustration; the inferior canine (fourth tooth from center, fig. 3) is larger than incisor 3 (third tooth from center).

As recorded by Thorpe, there are "but three teeth behind the canine in both jaws." There is no question that the "three teeth" are dP^2_2–dP^4_4. However, there is still a question whether the lack of P^1_1 is normal or abnormal for this individual. (See further discussion, p. 29.)

Scott[1] discussed the deciduous dentition of this same individual [which is actually an example of the Miniochoerinae] (S.D.S.M. 311) [31133] and based his conclusion on the genus *Merycoidodon* (p. 656) and stated: "*Milk Dentition:* (Pl. LXX, Fig. 1.) The only complete example of the temporary dentition that I have seen is contained in the beautiful young skull (No. 311) [31133] in the School of Mines Museum, Rapid City, S.D. This demonstrates that the formula is, as Leidy gave it: di^3_3, dc^1_1, dP^3_3, p1 having no predecessor." Scott corrected Leidy's formula, however; Leidy did not include inferior premolar one as "having no predecessor." What Leidy considered the lower canine was actually premolar one and his fourth incisor was the canine. Scott did not mention a connection between this immature specimen and the three associated individuals as did Thorpe.

Scott, on page 692 of his report, also discussed the deciduous dentition of *Leptauchenia* and concluded: "The *Milk Dentition* is preserved but seldom and I have seen no jaws in which the temporary incisors or canines are retained. One very young skull (Princeton Museum, No. 15,548) has the first set of cheek-teeth, above and below, with the first true molar already in place and the second one in process of eruption. There is no reason to doubt that in *Leptauchenia,* as in *Merycoidodon,* the formula should be written: dp^3_3 and the p^1 had no predecessor in the milk-series. It is highly probable also that the lower milk-canine, as in *Merycoidodon,* functioned as such and had not become, in shape and function, one of the incisors."

Scott's conclusions as to the function of the lower "milk-canine" is not indicated in his illustrations of the skull (S.D.S.M. 31133). The deciduous inferior canine seems to function anterior to the superior canine, the proper position between the two permanent canines which has been observed by the writers in all Merycoidodontinae.

Thorpe evidently did not come to a conclusion on the process of replacement of the milk dentition—either the first premolars are replaced or are permanent teeth that erupt after deciduous premolars 2–4 have erupted.

It is of interest that neither the Frick Laboratory nor the U.N.S.M. collections contain a specimen as juvenile as the S.D.S.M. Colorado specimen. The youngest individual in the two former collections is a skull and mandible (F:A.M. 72186B) referable to *Merycoidodon culbertsonii.* The dentition of this specimen is

$$\mathrm{dI}\frac{1\text{–}3}{1\text{–}3}\ \mathrm{dC/C},\ \mathrm{P}\frac{1\,(\text{erupt.})}{1\,(\text{alv.})},\ \mathrm{dP}\frac{2}{2}\text{–}\mathrm{M}\frac{1}{1}.$$

This specimen is older than the Colorado ex-

[1] 1940, pp. 656, 692, pl. 70, figs. 1, 1a, 1b.

ample in that M^1 is partially erupted and M_1 is erupted. P^1's, both left and right, are partially erupted, which suggests that there was not a predecessor to P^1. The P_1 on each side of the mandible is represented by an alveolus.

In the Miniochoerinae, the milk dentition is based on one individual. Also in *Merycoidodon*, there is just one specimen on which to base any conclusions. However, there is no evidence for or against dP_1.

In the genus *Brachycrus*, a skull (F:A.M. 57165) shows the P^1 in an erupting position and dP^2–M^1 erupting, which is not conclusive but at least suggests that P^1 had no predecessor.

In *Promerycochoerus carrikeri*, skull F:A.M. 42315 is immature, with P^1 alveolus on both sides. This specimen does not provide sufficient evidence regarding a deciduous P^1. However, it is of interest that, on the left side, both the deciduous and the permanent canines are in evidence.

The lower dentitions provide the writers with the same vexing problem. No example available to the writers is as juvenile as the Colorado specimen. In no instance has there been a mandibular ramus in the collections that lacks an alveolus for P_1. There are six examples of *Brachycrus* that contain the germs of P_1's but also possess perfectly shaped alveoli above the germs of the P_1's. Again, this is not conclusive, but suggests that the alveolus may have been present because of a dP_1. This same situation is true in *Ustatochoerus*. The mandible F:A.M. 43036 possesses P_1 germ and an alveolus above the germ.

The superior canines, both deciduous and permanent, are relatively large, and the roots curve posteriorly under P^1. This hardly allows space for the roots of dP^1 and also the germ of the permanent P^1. In the P_1, however, the circumstances are different. The P_1 is a large tooth with a curved root. The inferior canine is small and does not interfere with the space necessary for the root of a dP_1 and the germ of the permanent P_1.

It is apparent that dP^1 and dP_2 are lacking in the Miniochoerinae (based on the Colorado specimen, S.D.S.M. 31133) and dP^1 is absent from *Merycoidodon* (based on one specimen). The dP^1 is also absent from *Brachycrus*, and the dP_1 is questionably considered as being present in both *Brachycrus* and *Ustatochoerus* (based on examples each with a well-formed alveolus and with P_1 germ below the alveolus).

The present writers have observed several hundred immature skulls and mandibles with milk dentitions, and, in all cases in which the first premolars were present in both the skulls and mandibular rami, alveoli for the first premolars were obvious. Possibly the immature examples were not young enough for definite observations concerning the first premolars to be made. None of the specimens was so young as the Colorado example, S.D.S.M. 31133, of the Miniochoerinae, so more may be learned from the discovery of fetal or unusually young specimens. It would seem that milk dentitions of each of the 11 subfamilies should be studied before definite conclusions are made concerning whether dP^1 or dP_2 is present in all oreodonts. The present writers have concluded that the milk dentitions offer little in regard to the taxonomic revision of the oreodonts, but these teeth constitute one of the many interesting problems to research at a later date.[1] It has been difficult, in so many instances, to identify definitely the immature specimens specifically and even generically. Stratigraphic data associated with the specimens have often aided in our associating the immature with the mature forms. In the revision of the first eight subfamilies of the oreodonts, the present writers used dP^1 or dP_1 in instances in which the first premolar appeared too small to be a permanent tooth. Actually all may be permanent first premolars.[2]

The limb elements of the oreodonts are of fairly constant form and construction. They do vary, however, from being light to robust. Several of the Oligocene and lower Miocene species retained the fifth digit in the manus, but all forms appear to have only four digits in the

[1] Schultz plans to use the data concerning immature specimens that have been accumulated in the oreodont research during the past 30 years, and will prepare a report and illustrate typical examples from all 11 subfamilies.

[2] Miller and Wood (1963, p. 705) have published a paper (since this report was completed), on the upper deciduous molars in mid-Tertiary oreodonts, and have illustrated the upper milk teeth (P^{2-4}) of *Merycoidodon, Miniochoerus, Promerycochoerus, Merychyus, ?Oreodontoides, Hadroleptauchenia, Pseudocyclopidius*, and *Hypsiops*. They concluded that there was no dP^1 in the species and genera considered.

pes. Of course, good skeletal evidence is not available for all forms.

The writers have considered the matter of a detailed statistical analysis of the various oreodont remains, but, after some preliminary work, decided to leave this field of oreodont research to persons who are more statistically inclined.

Attention should be called to two papers, by Bader[1] and by Miller and Kahn,[2] which are concerned with the statistical analysis of the oreodont remains used in the present revision. Bader was interested primarily in the "variability and evolutionary rate in the oreodonts" and used the Merycochoerinae and the Merychyinae reports of the present writers[3] as well as the actual specimens in the collections of the Frick Laboratory and the University of Nebraska State Museum as the basis for his work. He concluded that "the evolutionary rates are considerably below comparable figures for metric characters in the evolution of the horse. The Merycochoerinae have a greater rate than in the Merychyinae in 19 of the 23 characters examined. The difference is statistically significant." The latter conclusion is demonstrated graphically with oreodont skulls in charts 18 and 18a of the present paper. In chart 18 the slowly evolving *Merychyus-Ticholeptus-Ustatochoerus* phylogenetic line is shown, and in chart 18a the *Merycochoerus-Brachycrus* line demonstrates a much greater rate of change. The former line showed very little change, except for a gradual increase in size during medial and late Miocene times, but the latter showed noticeable change in size and morphology during the same geologic period. The present writers do not agree with Bader concerning his comparisons of the evolutionary rates of the oreodonts and the horses. Very little has been published on the taxonomic revision of the horses based on precise stratigraphic data (oral communication from Morris F. Skinner of the Frick Laboratory). As a result there has been much "lumping" of material from unrelated species and even genera. A complete taxonomic revision of the horses is necessary before the comparative evolutionary rates can be properly evaluated.

[1] 1955, p. 119.
[2] 1962.
[3] 1940, p. 213; 1947, p. 157.

Miller and Kahn[4] used oreodonts as a basis for part of their discussion on multivariate analysis. They worked with material (Desmatochoerinae) published by the present writers[5] and with information provided by E. C. Olson, who had measured certain specimens in the Frick Laboratory and University of Nebraska State Museum collections with the idea of using the data later in a statistical study of the oreodonts. Schultz has discussed the report of Miller and Kahn with Leslie Marcus, who is also interested in making a statistical analysis of some of the oreodont material. Marcus, who is a qualified vertebrate paleontologist as well as a statistician, reported (written statement, June, 1963): "Miller and Kahn have used multivariate statistical analysis on four skull measurements of several species of oreodonts. They used only the oreodonts to illustrate the techniques they develop, and they reach no new conclusions concerning the relationships of the species included in their study. The oreodonts can be studied to advantage by multivariate analysis because of the abundance of well preserved and well documented specimens in several lineages. Multivariate techniques such as those discussed by Miller and Kahn will be useful in studying several characters simultaneously for descriptive purposes; for refined classification and identification; and for detailed evolutionary and stratigraphic interpretations." It is encouraging to know that several paleontologists plan to do further statistical analysis of the oreodont material.

Geographic Distribution

The Merycoidodontidae have been divided into 11 subfamilies, consisting of 46 genera, 14 subgenera, 127 species, 42 subspecies, and 10 varieties. In the present revision of the oreodonts, since 1940, the following have been described as new: 27 genera, 12 subgenera, 85 species, 27 subspecies, and 10 geologic and geographic varieties. Oreodont remains have been reported from 13 states of the United States (see charts 14, 17, and 20), from one locality in Canada, and from one site in the Canal Zone along the Panama Canal. The geologic distribu-

[4] 1962. Note that "*Megoreodon gigas loomisi*" (p. 261) should read "*Megoreodon grandis loomisi.*" This undoubtedly was a typographical error.
[5] 1954.

CHART 20

Geographic Distribution of the Merycoidodontidae in 13 States,[a] Showing the Number of Counties Within Each State in Which Specimens Have Been Found

	No. of Examples	California	Colorado	Idaho	Kansas	Montana	Nebraska	Nevada	New Mexico	North Dakota	Oregon	South Dakota	Texas	Wyoming
1. Merycochoerinae (1940,[b] this paper)														
Brachycrus	794	1	—	1	—	3	2	1	1	—	—	—	—	2
Merycochoerus	135	—	1	—	—	—	2	—	—	—	—	1	—	2
2. Ticholeptinae (1941, this paper)														
Ustatochoerus	338	2	2	—	1	1	9	1	2	—	—	4	3	—
Ticholeptus	148	1	—	1	—	1	3	2	—	—	1	—	1	—
Mediochoerus	4	—	—	—	—	—	2	—	—	—	—	—	—	—
3. Merychyinae (1947, this paper)														
Merychyus	887	1	2	—	—	2	6	—	1	—	—	2	1	4
M. (*Metoreodon*)	199	1	—	1	—	1	2	—	1	—	—	—	—	—
Paramerychyus	5	—	—	—	—	—	—	—	—	—	—	1	—	1
Oreodontoides	16	—	—	—	—	—	—	—	—	—	1	1	—	—
O. (*Paroreodon*)	20	—	—	—	—	—	—	—	—	—	1	—	—	—
4. Promerycochoerinae (1949)														
Promerycochoerus	154	—	—	—	—	1	2	—	—	—	1	3	—	2
P. (*Parapromerycochoerus*)	21	—	—	—	—	—	—	—	—	—	1	2	—	1
P. (*Pseudopromerycochoerus*)	35	—	—	—	—	2	—	—	—	—	1	3	—	1
Mesoreodon	110	1	—	—	—	2	2	—	—	—	—	—	—	2
Promesoreodon	5	—	—	—	—	—	—	—	—	—	—	2	—	—
Merycoides	6	—	—	—	—	1	1	—	—	—	—	—	—	1
5. Phenacocoelinae (1950)														
Phenacocoelus	48	—	—	—	—	—	1	—	—	—	—	1	—	3
Hypsiops	28	1	—	—	—	2	1	—	—	—	1	—	—	1
Submerycochoerus	3	—	—	—	—	1	—	—	—	—	—	—	—	—
Pseudomesoreodon	5	—	—	—	—	2	—	—	—	—	—	—	—	—
6. Desmatochoerinae (1954, this paper)														
Megoreodon	56	—	—	—	—	1	2	—	—	—	—	—	—	2
Desmatochoerus	63	—	—	—	—	3	2	—	—	—	1	2	—	2
D. (*Paradesmatochoerus*)	43	1	—	—	—	—	3	—	—	—	—	3	—	3
Pseudodesmatochoerus	25	—	—	—	—	3	—	—	—	—	1	—	—	2
Superdesmatochoerus	10	—	—	—	—	—	—	—	—	—	1	—	—	—
Subdesmatochoerus	20	—	—	—	—	1	2	—	—	—	—	3	—	—
Prodesmatochoerus	24	—	—	—	—	—	—	—	—	—	—	1	—	3
7. Miniochoerinae (1956, this paper)														
Miniochoerus	38	—	1	—	—	—	2	—	—	1	—	3	—	1
M. (*Paraminiochoerus*)	270	—	2	—	—	—	3	—	—	1	—	3	—	3
Platyochoerus	87	—	1	—	—	—	3	—	—	1	—	1	—	2
Stenopsochoerus	44	—	1	—	—	—	2	—	—	—	—	—	—	2
S. (*Pseudostenopsochoerus*)	34	—	2	—	—	—	1	—	—	—	—	—	—	2
Parastenopsochoerus	2	—	—	—	—	—	—	—	—	—	—	—	—	1

CHART 20—(*Continued*)

	No. of Examples	California	Colorado	Idaho	Kansas	Montana	Nebraska	Nevada	New Mexico	North Dakota	Oregon	South Dakota	Texas	Wyoming
8. Oreonetinae[c] (1956, this paper)														
Oreonetes	17	—	—	—	—	3	—	—	—	—	—	—	—	—
Limnenetes	5	—	—	—	—	2	—	—	—	—	—	—	1	—
Bathygenys	6	—	—	—	—	1	—	—	—	—	—	—	—	1
9. Merycoidodontinae (this paper)														
Merycoidodon	445	—	1	—	—	2	3	—	—	1	—	5	—	3
M. (*Anomerycoidodon*)	34	—	—	—	—	—	1	—	—	1	—	4	—	—
M. (*Blickohyus*)	29	—	1	—	—	—	1	—	—	—	—	4	—	—
Paramerycoidodon	38	—	—	—	—	—	1	—	—	1	—	2	—	1
P. (*Barbourochoerus*)	58	—	—	—	—	—	1	—	—	—	—	4	—	—
P. (*Gregoryochoerus*)	51	—	—	—	—	1	3	—	—	—	—	5	—	—
Otionohyus	108	—	—	—	—	—	3	—	—	1	—	4	—	2
O. (*Otarohyus*)	111	—	2	—	—	1	2	—	—	1	—	5	—	—
Genetochoerus	43	—	1	—	—	—	3	—	—	—	—	2	—	2
G. (*Osbornohyus*)	52	—	—	—	—	—	1	—	—	1	—	4	—	—
Pseudogenetochoerus	44	—	—	—	—	—	—	—	—	—	1	—	—	—
Epigenetochoerus	5	—	—	—	—	—	—	—	—	—	1	—	—	—
10. *Eporeodontinae* (this paper)														
Eporeodon	14	—	—	—	—	—	—	—	—	—	1	—	—	—
E. (*Paraeporeodon*)	95	—	—	—	—	—	—	—	—	—	1	—	—	—
Dayohyus	19	—	—	—	—	—	—	—	—	—	1	—	—	—
11. Leptauchiniinae (this paper)														
Sespia	101	1	1	—	—	1	3	—	—	—	—	1	—	3
Megasespia	14	—	—	—	—	—	3	—	—	—	—	—	—	1
Pithecistes	168	—	—	—	—	1	3	—	—	—	—	3	—	3
Leptauchenia	209	—	—	—	—	—	7	—	—	—	—	4	—	3
Cyclopidius	82	—	—	—	—	3	—	—	—	—	—	—	—	—
Hadroleptauchenia	207	—	—	—	—	—	6	—	—	—	—	5	—	3
Pseudocyclopidius	248	—	1	—	—	1	4	—	—	—	—	3	—	4

[a] Records from Panama Canal Zone and Canada not included.
[b] Dates in this column refer to publications by Schultz and Falkenbach.
[c] Two additional genera (*Megabathygenys* and *Parabathygenys*) are described (based on specimens from Wyoming) in the present paper.

tion is from early Oligocene through medial Pliocene (see chart 13).

Gazin[1] recently reported that no oreodonts were evident in the Eocene. (See discussion, this report, p. 399). The present writers believe that a revision of the agriochoerids will present evidence which will show that some of these do have a close relationship with the oreodonts.

[1] 1955, pp. 31-40.

Explanation of Chart 20: The geographic distribution of the oreodonts is shown in chart 17 (p. 422). A detailed distribution is presented in chart 20 (p. 438). The latter includes genera, number of available examples, and the states and the number of counties in which the examples of each genus were found.

As stated in the explanation of chart 17, the geographic distribution of the Merycoidodontidae is restricted to 13 of the 50 states in the United States, and one locality in Canada.

Although the oreodonts were very numerous, as is evidenced by the variety and quantity of remains, the family is not known outside North America. Oreodont examples are found in the same areas, quarries, and formations as those of horses (Equidae) and camels (Camelidae). The latter two groups migrated to other continents, but the oreodonts seem to have evolved strictly in North America. (The camels evolved locally but also migrated to other continents after the oreodonts became extinct).

Subfamily Relationships

The relationship between all 11 subfamilies of the oreodonts is not clearly understood. Definite relationship between certain subfamilies seems obvious (based on geologic occurrence and morphologic characters), but additional evidence is needed for the connecting links between some groups. (Chart 14, pp. 416–417, indicates definite and possible relationships.) The following is a resume of the relationships:

Merycochoerinae, subfamily 1, derived from examples of Phenacocoelinae, subfamily 5.

Ticholeptinae, subfamily 2, from Merychyinae, subfamily 3.

Merychyinae, subfamily 3, gave rise to Phenacocoelinae and Ticholeptinae; its ancestral form is questionable.

Promerycochoerinae, subfamily 4, from Merycoidodontinae.

Phenacocoelinae, subfamily 5, from Merychyinae, and giving rise to Merycochoerinae.

Desmatochoerinae, subfamily 6 (longest known phylum of oreodont), possibly derived from Merycoidontinae.

Miniochoerinae, subfamily 7, no apparent relationship noted (dentition similar to that of Leptaucheniinae).

Oreonetinae, subfamily 8 (shortest known phylum), no apparent alliance.

Merycoidodontinae, subfamily 9, gave rise to Promerycochoerinae, and possibly Eporeodontinae; probably derived from same ancestral group as that of Desmatochoerinae.

Eporeodontinae, subfamily 10 (perhaps as short a phylum as that of Oreonetinae), possibly derived from Merycoidodontinae.

Leptaucheniinae, subfamily 11 (most unique oreodont), no apparent relationship (dentition similar to that of Miniochoerinae), but possibly derived from Oreonetinae.

The largest oreodont skulls are recorded in the genus *Megoreodon* of the subfamily Desmatochoerinae from the Gering and Monroe Creek formations, or their equivalents in age. The smallest skulls are found in *Bathygenys alpha* of the Oreonetinae from deposits of oreodont faunal "Zone B" of the Chadron.

Much of the problem of relationship between subfamilies is probably due to the hiatuses between the various formations or members and also, in part, to the paleoecologic circumstances. This seems evident in the uppermost portion of faunal "Zone D" of the Brule in Nebraska, where sediments yield primarily the remains of the leptauchenins. The dry, loess-like sediments of these particular beds indicate an extremely arid period. The leptauchenins apparently were adapted for desert conditions, and most of the other oreodonts that lived at that time migrated to localities with more favorable living conditions. Migration also must be considered in establishing phylogenetic relationships. Some oreodonts migrated in and out of areas as ecological conditions changed. Conditions for the preservation of the remains of the animals were not always favorable in all of the localities; hence there are many gaps in the phylogeny of the oreodonts.

The paleosols indicate that there were long periods when few bones could be preserved. The old soils no doubt suggest a more or less static condition as far as deposition is concerned and represent a period of weathering and leaching.

Key Characters of the Merycoidodontidae

Three different keys are here presented: one based on various combinations of skull characters (chart 21); one giving the range of the basal lengths of the skulls (chart 22); and one listing the species of each genus or subgenus possessing the smallest and largest third upper molars (chart 23, and figs. 48–53, in which the third upper molars with little or no wear have been illustrated).

Explanation of Chart 21: A proposed key to certain characters of the skulls of the Merycoidodontidae is used as the basis for chart 21. These characters are listed, and an "x" indicates their presence in a certain subfamily. The "x" may be accompanied by a plus or minus sign to indicate that the characters are developed more or less than average.

CHART 21

KEY CHARACTERS OF THE SKULLS OF THE 11 SUBFAMILIES OF THE MERYCOIDODONTIDAE[a]

	1. Merycochoerinae, 1940[b]	2. Ticholeptinae, 1941	3. Merychyinae, 1947	4. Promerycochoerinae, 1949	5. Phenacocoelinae, 1950	6. Desmatochoerinae, 1954	7. Miniochoerinae, 1956	8. Oreonetinae, 1956	9. Merycoidodontinae, This Paper	10. Eporeodontinae, This Paper	11. Leptaucheniinae, This Paper
Basal length of skull											
Minimum	222	179	123	149	155	155	107	70	153	170	72
Maximum	330	288	178	350	287	357	168	100	234	228	145
Width of skull											
Minimum	161	123	72	112	90	80	64	38	84	125	52
Maximum	291	218	132	322	187	245	108	65	180	160	113
Height of skull											
Low	—	x	—	x	x	—	x	—	x	x	x
Medium	x	x	x	—	x	x	x	x	x	x	—
High	x	—	—	x	—	x	—	—	x	—	—
Occipital region											
Fan-shaped	x	x	−x+	—	−x	—	x	x	—	—	x
Posteriorly produced	—	—	—	x	—	x	—	—	x	x	—
Nasals											
Slightly retracted	—	—	x	x	x	x	x	x	x	x	x
Moderately retracted	x	x	—	—	x	—	—	—	—	—	—
Greatly retracted	x	x	—	—	—	—	—	—	—	—	—
Lacrimal fossa											
Small	—	x	x	x	—	x	x	x	—	—	x
Large	x	x	—	—	x	x	—	x	—	x	—
Shallow	—	x	−x+	x	—	—	x	x	—	—	—
Deep	x	x	x	—	x	x	x	x	—	x	—
Vacuities											
Occipital	—	—	—	—	—	x[c]	—	—	—	—	—
Facial	—	x	x	—	x	x[c]	—	—	—	—	—
Nasal-facial	—	—	—	—	—	—	—	—	—	—	x
Supraorbital	—	−x	—	—	—	—	—	—	—	—	—
Bullae											
Minute	—	—	—	—	—	x	x	—	x	—	—
Inflated											
Moderately	—	x	—	x	−x	—	—	—	x	x	x
Greatly	—	—	x	—	x	x	—	x	x	x	—
Depressed	—	x	—	—	x+	—	—	—	—	—	—
Inflated, small base	x	—	—	—	—	—	—	—	—	—	—
Dentition											
Brachyodont	−x+	x+	x	x	x	x	x	x	x	x	—
Subhypsodont	—	x	x	—	−x	—	—	—	—	—	—
Hypsodont	—	—	—	—	—	—	—	—	—	—	x
Extremely hypsodont	—	—	—	—	—	—	—	—	—	—	x
Molar fossettes shallow	—	—	—	—	—	—	x	—	—	—	x
Molar fossettes deep	x	x	x	x	x	x	—	x	x	x	—

[a] All measurements in millimeters.
[b] These dates are those of the publication of the Schultz and Falkenbach revisions.
[c] May or may not be present.

CHART 22

MERYCOIDODONTIDAE. SKULL MEASUREMENTS[a] (SMALLEST TO LARGEST) OF GENERA AND SUBGENERA, WITH GEOLOGICAL OCCURRENCE

Genus or Subgenus	Subfamily No. and Year Published	Total No. of Examples	Range in Basal Lengths of Skulls	Chadron "B"	Chadron "C"	Chadron "A"	Brule "B"	Brule "C"	Brule "D"	Gering	Monroe Creek	Harrison	Marsland	"Sheep Creek"	"Lower Snake Creek"	Valentine	Ash Hollow
Bathygenys	8;1956	6	((70))	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Sespia	11; this paper	111	72.5–81	—	—	—	—	—	—	x	x	—	—	—	—	—	—
Pithecistes	11; this paper	164	((89))–96	—	—	—	—	—	x	x	x	—	—	—	—	—	—
Leptauchenia	11; this paper	307	((90))–((107))	—	—	—	—	x	x	x	x	—	—	—	—	—	—
Megasespia	11; this paper	13	((92))	—	—	—	—	—	—	x	—	—	—	—	—	—	—
Pseudocyclopidius	11; this paper	253	(93)–((135))	—	—	x	—	—	x	x	—	—	—	—	—	—	—
Limnenetes	8; 1956	5	((96))	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Oreonetes	8; 1956	17	(100)	x	—	—	—	—	—	—	—	—	—	—	—	—	—
Hadroleptauchenia	11; this paper	206	101–((118))	—	—	x	x	—	x	x	—	—	—	—	—	—	—
Miniochoerus (Paraminiochoerus)	8; 1956	270	103–147	—	—	x	x	x	—	—	—	—	—	—	—	—	—
Cyclopidius	11; this paper	52	((111))–((125))	—	—	—	—	—	—	x	—	—	—	—	—	—	—
Merychyus	3; 1947	887	123–178	—	—	—	—	—	—	—	—	x	x	—	—	—	—
Stenopsochoerus	8; 1956	44	124–161	—	—	x	—	x	—	—	—	—	—	—	—	—	—
Platyochoerus	8; 1956	87	129–169	—	—	—	x	—	—	—	—	—	—	—	—	—	—
(Parastenopsochoerus)	8; 1956	2	134–137	—	—	x	—	—	—	—	—	—	—	—	—	—	—
Stenopsochoerus (Pseudostenopsochoerus)	8; 1956	34	135–153	—	x	x	—	—	—	—	—	—	—	—	—	—	—
Miniochoerus	8; 1956	38	137–168	—	—	x	x	x	x	—	—	—	—	—	—	—	—
Oreodontoides (Paroreodon)	3; 1947	20	140–161	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Merychyus (Metoreodon)	3; 1947	199	147–152	—	—	—	—	—	—	—	—	—	—	x	x	—	—
Genetochoerus	9; this paper	43	153–173	—	—	x	—	—	—	—	—	—	—	—	—	—	—
Phenacocoelus	5; 1950	48	155–255	—	—	—	—	—	—	—	—	x	x	—	—	—	—
Otionohyus	9; this paper	108	156–173	—	—	x	—	—	—	—	—	—	—	—	—	—	—
Oreodontoides	3; 1947	16	158–160	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Epigenetochoerus	9; this paper	5	160	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Merycoidodon	9; this paper	445	160–208	x	x	x	—	—	—	—	—	—	—	—	—	—	—
Genetochoerus (Osbornohyus)	9; this paper	52	163–180	—	—	—	x	x	x	—	—	—	—	—	—	—	—
Otionohyus (Otarohyus)	9; this paper	111	163–205	—	—	—	x	x	x	—	—	—	—	—	—	—	—

CHART 22—(*Continued*)

Genus or Subgenus	Subfamily No. and Year Published	Total No. of Examples	Range in Basal Lengths of Skulls	Chadron "B"	Chadron "C"	Chadron "A"	Brule "B"	Brule "C"	Brule "D"	Gering	Monroe Creek	Harrison	Marsland	"Sheep Creek"	"Lower Snake Creek"	Valentine	Ash Hollow
Paramerychyus	3; 1947	5	164–170	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Dayohyus	10; this paper	19	170–200	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Eporeodon	10; this paper	14	171–207	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Prodesmatochoerus	6; 1954	24	173–190	—	—	x	—	—	—	—	—	—	—	—	—	—	—
Merycoides	3; 1949	6	176–247	—	—	—	—	—	—	x	x	—	—	—	—	—	—
Ticholeptus	2; 1941	148	179–210	—	—	—	—	—	—	—	—	—	—	x	x	—	—
Subdesmatochoerus	6; 1954	20	180–215	—	—	—	x	—	x	—	—	—	—	—	—	—	—
Mediochoerus	2; 1941	4	182–195	—	—	—	—	—	—	—	—	—	x	—	x	—	—
Merycoidodon (*Blickohyus*)	9; this paper	29	182–205	—	—	—	—	x	x	—	—	—	—	—	—	—	—
Paramerycoidodon	9; this paper	38	183–206	—	—	x	—	—	—	—	—	—	—	—	—	—	—
Hypsiops	5; 1950	28	183–229	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Promesoreodon	4; 1949	5	185–195	—	—	—	—	—	x	—	—	—	—	—	—	—	—
Paramerycoidodon (*Gregoryochoerus*)	9; this paper	51	190–210	—	—	—	—	—	x	x	—	—	—	—	—	—	—
Merycoidodon (*Anomerycoidodon*)	9; this paper	34	190–211	—	—	—	x	—	x	—	—	—	—	—	—	—	—
Paramerycoidodon (*Barbourochoerus*)	9; this paper	58	197–234	—	—	—	x	—	x	—	—	—	—	—	—	—	—
Mesoreodon	4; 1949	110	200–259	—	—	—	—	—	—	x	x	—	—	—	—	—	—
Ustatochoerus	2; 1941	338	202–288	—	—	—	—	—	—	—	—	—	—	—	—	x	x
Eporeodon (*Paraeporeodon*)	10; this paper	95	208–228	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Desmatochoerus (*Paradesmatochoerus*)	6; 1954	43	215–236	—	—	—	—	—	—	x	x	—	—	—	—	—	—
Promerycochoerus (*Pseudopromerycochoerus*)	4; 1949	35	221–355	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Brachycrus	1; 1940	794	222–290	—	—	—	—	—	—	—	—	—	—	x	x	—	—
Pseudodesmatochoerus	6; 1954	25	233–257	—	—	—	—	—	—	x	x	x	—	—	—	—	—
Desmatochoerus	6; 1954	63	233–285	—	—	—	—	—	—	x	x	x	—	x	—	—	—
Pseudomesoreodon	5; 1950	5	237–287	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Merycochoerus	1; 1940	135	237–330	—	—	—	—	—	—	—	—	—	x	—	—	—	—
Megoreodon	6; 1954	56	246–357	—	—	—	—	—	—	x	x	—	—	—	—	—	—
Submerycochoerus	5; 1950	3	250	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Promerycochoerus	4; 1949	154	266–350	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Promerycochoerus (*Parapromerycochoerus*)	4; 1949	21	276–325	—	—	—	—	—	—	—	—	x	—	—	—	—	—
Superdesmatochoerus	6; 1954	10	306–320	—	—	—	—	—	—	—	—	x	—	—	—	—	—

[a] ( ), Approximate; (( )), estimated. All measurements in millimeters.

CHART 23

Key to the Identification of Third Upper Molars and Their Geologic Occurrences as Illustrated in Figures 48–53[a]

	Faunal Zones, Formations, or Their Equivalents in Age														
	Chadron "B"	Chadron "C"	Brule "A"	Brule "B"	Brule "C"	Brule "D"	Gering	Monroe Creek	Harrison	Lower Marsland	Upper Marsland	"Sheep Creek"	"Lower Snake Creek"	Valentine	Ash Hollow
1. Merycochoerinae: 1940,[b] this paper, fig. 48															
Brachycrus siouense, F:A.M. 36113	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—
Brachycrus wilsoni, F:A.M. 34202	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—
Merycochoerus proprius, F:A.M. 424690	—	—	—	—	—	—	—	—	—	—	3	—	—	—	—
M. matthewi, F:A.M. 33317	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—
2. Ticholeptinae, 1941, this paper, fig. 48															
Ustatochoerus major, F:A.M. 34221	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5
U. medius, F:A.M. 43030A	—	—	—	—	—	—	—	—	—	—	—	—	—	6	—
Ticholeptus hypsodus, F:A.M. 43044	—	—	—	—	—	—	—	—	—	—	—	—	7	—	—
T. tooheyi, U.N.S.M. 1-15-9-36	—	—	—	—	—	—	—	—	—	—	—	8	—	—	—
Mediochoerus blicki, F:A.M. 43172	—	—	—	—	—	—	—	—	—	—	—	—	9	—	—
M. johnsoni, U.N.S.M. 2-11-8-36	—	—	—	—	—	—	—	—	—	—	10	—	—	—	—
3. Merychyinae, 1947, this paper, figs. 48, 49															
Merychyus (Metoreodon) relictus, F:A.M. 43079	—	—	—	—	—	—	—	—	—	—	—	—	11	—	—
M. (M.) relictus taylori, F:A.M. 34319	—	—	—	—	—	—	—	—	—	—	—	12	—	—	—
Merychyus elegans, U.N.S.M. 2-10-8-30	—	—	—	—	—	—	—	—	—	—	13	—	—	—	—
M. crabilli, F:A.M. 43391	—	—	—	—	—	—	—	—	14	—	—	—	—	—	—
Paramerychyus harrisonensis, F:A.M. 33314	—	—	—	—	—	—	—	—	15	—	—	—	—	—	—
P. relictus, A.M. 13813	—	—	—	—	—	—	—	—	16	—	—	—	—	—	—
Oreodontoides oregonensis, A.M. 7513	—	—	—	—	—	—	—	—	17	—	—	—	—	—	—
O. curtus, A.M. 13817	—	—	—	—	—	—	—	—	18	—	—	—	—	—	—
O. (Paroreodon) stocki, A.M. 7814	—	—	—	—	—	—	—	—	19	—	—	—	—	—	—
4. Promerycochoerinae, 1949, this paper, figs. 49, 50															
Promerycochoerus carrikeri, F:A.M. 42312	—	—	—	—	—	—	—	—	20	—	—	—	—	—	—
P. superbus, A.M. 7445	—	—	—	—	—	—	—	—	21	—	—	—	—	—	—
P. (Parapromerycochoerus) barbouri, F:A.M. 33315	—	—	—	—	—	—	—	—	22	—	—	—	—	—	—
P. (P.) macrostegus, A.M. 7450	—	—	—	—	—	—	—	—	23	—	—	—	—	—	—
P. (Pseudopromerycochoerus) minor, C. M. 769	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—
P. (P.) montanus pinensis, A.M. 12945	—	—	—	—	—	—	—	—	25	—	—	—	—	—	—
Mesoreodon megalodon, F:A.M. 33336	—	—	—	—	—	—	—	26	—	—	—	—	—	—	—
M. cheeki, F:A.M. 33359	—	—	—	—	—	—	27	—	—	—	—	—	—	—	—
Promesoreodon scanloni, F:A.M. 45354 rev.	—	—	—	—	—	28	—	—	—	—	—	—	—	—	—
Merycoides giganteus, F:A.M. 33316	—	—	—	—	—	—	—	29	—	—	—	—	—	—	—
M. nebraskensis, F:A.M. 33363	—	—	—	—	—	—	30	—	—	—	—	—	—	—	—
5. Phenacocoelinae, 1950, this paper, fig. 50															
Phenacocoelus stouti, F:A.M. 44839	—	—	—	—	—	—	—	—	—	31	—	—	—	—	—
P. typus, F:A.M. 33397	—	—	—	—	—	—	—	—	32	—	—	—	—	—	—
Hypsiops brachymelis, F:A.M. 34401	—	—	—	—	—	—	—	—	33	—	—	—	—	—	—
H. luskensis, F:A.M. 44853A	—	—	—	—	—	—	—	—	34	—	—	—	—	—	—
Submerycochoerus bannackensis, F:A.M. 34317	—	—	—	—	—	—	—	—	35	—	—	—	—	—	—
Pseudomesoreodon rooneyi, F:A.M. 44948A	—	—	—	—	—	—	—	—	36	—	—	—	—	—	—
P. rolli, F:A.M. 34481	—	—	—	—	—	—	—	—	37	—	—	—	—	—	—

CHART 23—(*Continued*)

	Faunal Zones, Formations, or Their Equivalents in Age														
	Chadron "B"	Chadron "C"	Brule "A"	Brule "B"	Brule "C"	Brule "D"	Gering	Monroe Creek	Harrison	Lower Marsland	Upper Marsland	"Sheep Creek"	"Lower Snake Creek"	Valentine	Ash Hollow
6. Desmatochoerinae, 1954, this paper, figs. 50, 51															
Megoreodon fricki, F:A.M. 33308	—	—	—	—	—	—	—	38	—	—	—	—	—	—	—
M. grandis loomisi, F:A.M. 42321	—	—	—	—	—	—	39	—	—	—	—	—	—	—	—
Desmatochoerus curvidens gregoryi, F:A.M. 37211	—	—	—	—	—	—	—	—	40	—	—	—	—	—	—
Desmatochoerus hatcheri geringensis, F:A.M. 43316	—	—	—	—	—	—	41	—	—	—	—	—	—	—	—
D. (*Paradesmatochoerus*) *sanfordi*, F:A.M. 49636	—	—	—	—	—	—	42	—	—	—	—	—	—	—	—
D. (*P.*) *wyomingensis* F:A.M. 37571	—	—	—	—	—	—	43	—	—	—	—	—	—	—	—
Pseudodesmatochoerus wascoensis, A.M. 7827	—	—	—	—	—	—	—	—	44	—	—	—	—	—	—
P. hoffmani, F:A.M. 45456	—	—	—	—	—	—	—	45	—	—	—	—	—	—	—
Superdesmatochoerus lulli, A.M. 7469	—	—	—	—	—	—	—	—	46	—	—	—	—	—	—
Subdesmatochoerus shannonensis, F:A.M. 49550	—	—	—	—	—	47	—	—	—	—	—	—	—	—	—
S. socialis, F:A.M. 45177	—	—	—	48	—	—	—	—	—	—	—	—	—	—	—
Prodesmatochoerus meekae, F:A.M. 49549	—	—	49	—	—	—	—	—	—	—	—	—	—	—	—
7. Miniochoerinae, 1956, this paper, fig. 51															
Miniochoerus cheyennensis, A.M. 9797	—	—	—	—	—	50	—	—	—	—	—	—	—	—	—
M. battlecreekensis, U.N.S.M. 28044	—	—	51	—	—	—	—	—	—	—	—	—	—	—	—
M. (*Paraminiochoerus*) *ottensi*, F:A.M. 49546	—	—	—	—	52	—	—	—	—	—	—	—	—	—	—
M. (*P.*) *gracilis*, U.N.S.M. 28140	—	—	53	—	—	—	—	—	—	—	—	—	—	—	—
Platyochoerus hatcreekensis, U.N.S.M. 28511	—	—	—	—	54	—	—	—	—	—	—	—	—	—	—
P. platycephalus, F:A.M. 45089	—	—	55	—	—	—	—	—	—	—	—	—	—	—	—
Stenopsochoerus berardae, F:A.M. 49617	—	—	—	—	56	—	—	—	—	—	—	—	—	—	—
S. sternbergi, F:A.M. 44980	—	—	57	—	—	—	—	—	—	—	—	—	—	—	—
S. (*Pseudostenopsochoerus*) *chadronensis*, var., F:A.M. 45489	—	—	58	—	—	—	—	—	—	—	—	—	—	—	—
S. (*P.*) *reideri*, F:A.M. 49620	—	59	—	—	—	—	—	—	—	—	—	—	—	—	—
Parastenopsochoerus conversensis, F:A.M. 45011	—	—	60	—	—	—	—	—	—	—	—	—	—	—	—
8. Oreonetinae, 1956, this paper, fig. 51															
Bathygenys alpha, F:A.M. 45334	61	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Limnenetes platyceps, A.M. 9729	62	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Oreonetes anceps, C.M. 745	63	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9. Merycoidodontinae, this paper, figs. 51, 52															
Merycoidodon culbertsonii, F:A.M. 45159	—	—	64	—	—	—	—	—	—	—	—	—	—	—	—
M. forsythae, F:A.M. 72303	65	—	—	—	—	—	—	—	—	—	—	—	—	—	—
M. (*Anomerycoidodon*) *lambi*, F:A.M. 72139	—	—	—	—	—	66	—	—	—	—	—	—	—	—	—
M. (*A.*) *dani*, F:A.M. 72132	—	—	—	67	—	—	—	—	—	—	—	—	—	—	—
Merycoidodon (*Blickohyus*) *lynchi*, F:A.M. 45297	—	—	—	—	—	68	—	—	—	—	—	—	—	—	—
M. (*B.*) *galushai*, F:A.M. 45279	—	—	—	—	69	—	—	—	—	—	—	—	—	—	—
Paramerycoidodon georgei, F:A.M. 45143	—	—	70	—	—	—	—	—	—	—	—	—	—	—	—
P. (*Barbourochoerus*) *major*, A.M. 1038	—	—	—	—	—	71	—	—	—	—	—	—	—	—	—
P. (*B.*) *bacai*, U.N.S.M. 28191	—	—	—	72	—	—	—	—	—	—	—	—	—	—	—
P. (*Gregoryochoerus*) *meagherensis*, F:A.M. 45462	—	—	—	—	—	—	73	—	—	—	—	—	—	—	—

CHART 23—(*Continued*)

	Faunal Zones, Formations, or Their Equivalents in Age														
	Chadron "B"	Chadron "C"	Brule "A"	Brule "B"	Brule "C"	Brule "D"	Gering	Monroe Creek	Harrison	Lower Marsland	Upper Marsland	"Sheep Creek"	"Lower Snake Creek"	Valentine	Ash Hollow
P. (*G.*) *wanlessi*, F:A.M. 72109	—	—	—	—	—	74	—	—	—	—	—	—	—	—	—
Otionohyus wardi, F:A.M. 45015	—	—	75	—	—	—	—	—	—	—	—	—	—	—	—
O. w. degrooti, F:A.M. 49760	—	76	—	—	—	—	—	—	—	—	—	—	—	—	—
O. (*Otarohyus*) *alexi*, F:A.M. 72060	—	—	—	—	—	77	—	—	—	—	—	—	—	—	—
O. (*O.*) *bullatus*, F:A.M. 45267	—	—	—	78	—	—	—	—	—	—	—	—	—	—	—
Genetochoerus periculorum, A.M. 6397	—	—	79	—	—	—	—	—	—	—	—	—	—	—	—
G. (*Osbornohyus*) *dickinsonensis*, C.M. 1584	—	—	—	—	—	80	—	—	—	—	—	—	—	—	—
G. (*O.*) *norbeckensis*, F:A.M. 49733	—	—	—	81	—	—	—	—	—	—	—	—	—	—	—
Pseudogenetochoerus covensis, C.I.T. 2688	—	—	—	—	—	—	—	—	82	—	—	—	—	—	—
P. condoni, A.M. 7881	—	—	—	—	—	—	—	—	83	—	—	—	—	—	—
Epigenetochoerus parvus, Y.P.M. 12420	—	—	—	—	—	—	—	—	84	—	—	—	—	—	—
10. Eporeodontinae, this paper, fig. 53															
Eporeodon davisi, A.M. 7622	—	—	—	—	—	—	—	—	85	—	—	—	—	—	—
E. occidentalis, Y.P.M. 10142	—	—	—	—	—	—	—	—	86	—	—	—	—	—	—
E. (*Paraeporeodon*) *longifrons*, A.M. 7567	—	—	—	—	—	—	—	—	87	—	—	—	—	—	—
E. (*P.*) *pacificus*, A.M. 7777	—	—	—	—	—	—	—	—	88	—	—	—	—	—	—
Dayohyus trigonocephalus, A.M. 7693	—	—	—	—	—	—	—	—	89	—	—	—	—	—	—
D. wortmani, U.C. 1911	—	—	—	—	—	—	—	—	90	—	—	—	—	—	—
11. Leptaucheniinae, this paper, fig. 54															
Sespia marianae, U.N.S.M. 28448	—	—	—	—	—	—	91	—	—	—	—	—	—	—	—
S. ultima, F:A.M. 45625	—	—	—	—	—	—	—	92	—	—	—	—	—	—	—
Megasespia middleswarti, U.N.S.M. 28408	—	—	—	—	—	—	93	—	—	—	—	—	—	—	—
Pithecistes tanneri, U.N.S.M. 28492	—	—	—	—	—	94	—	—	—	—	—	—	—	—	—
P. copei, F:A.M. 56733	—	—	—	—	—	—	—	95	—	—	—	—	—	—	—
Leptauchenia decora, F:A.M. 45503	—	—	—	—	—	96	—	—	—	—	—	—	—	—	—
L. margeryae, F:A.M. 45632	—	—	—	—	—	—	—	97	—	—	—	—	—	—	—
Hadroleptauchenia primitiva, F:A.M. 45571A	—	—	—	—	—	98	—	—	—	—	—	—	—	—	—
H. densa, F:A.M. 56901A	—	—	—	—	—	—	99	—	—	—	—	—	—	—	—
Pseudocyclopidius frankforteri, F:A.M. 45554	—	—	—	—	—	100	—	—	—	—	—	—	—	—	—
P. lullianus expiratus, F:A.M. 45601	—	—	—	—	—	—	—	101	—	—	—	—	—	—	—

[a] The arabic numbers in the body of this chart coincide with those on figures 48–53.
[b] The dates in this column are those of the respective reports by Schultz and Falkenbach.

It should be noted that some of the same characters may appear in several lines; however, a combination of characters forms the basis for the distinguishing of a subfamily. In some instances, for example, the length and retraction of the nasals of the Merycochoerinae are diagnostic not only as generic but also as specific characters. The nasal-facial vacuities and the height of crowns of the molars are primary among the characters of the Leptaucheniinae. The exoccipital vacuities are outstanding in most of the Desmatochoerinae. The difference in minute and inflated bullae is also readily recognized. The shallow molar fossettes of the Miniochoerinae and the Leptaucheniinae are diagnostically different from the deep fossettes of other subfamilies.

EXPLANATION OF CHART 22: The range in the basal lengths of the skulls of the various genera and subgenera is recorded in chart 22 from smallest to largest (regardless of subfamily relationship or geologic sequence). The dates of published revisions of the various subfamilies by Schultz and Falkenbach, the total number of examples (including those of which the basal lengths are not preserved), and the geologic range are also given.

The information on this chart supplements that of chart 21. If the basal length is available for any example, the generic and subgeneric identification is made easier. If the geologic occurrence of the particular sample also is known, the identification can be further narrowed.

EXPLANATION OF CHART 23: The vertical length, anterior-posterior length, and the crown view of M^3 are helpful characters in the determination of the identification of an oreodont skull as to genus and subgenus. That is, with the aid of a third upper molar, one may place the form within the proper phylogenetic line. In chart 23 are listed the subfamilies (with the year of the published revision by Schultz and Falkenbach), genera, species, and index numbers for species. The species that possess the smallest and largest upper molars of each genus or subgenus are also listed; examples of the third upper molars (smallest and largest) are illustrated in figures 48–53. The lateral and occlusal views are shown in the figures, and the code numbers 1–101 appear on chart 23. These code numbers indicate the generic and specific identifications and are placed in the columns to indicate approximate geologic distributions.

Figures 48–53 are in outline, with stippled areas to indicate amount of wear.

EXPLANATION OF TEXT FIGURES 48–53

FIG. 48. Lateral and occlusal views of M^3:

1. Merycochoerinae:
 1. *Brachycrus siouense,* F:A.M. 36113 ("Lower Snake Creek")
 2. *Brachycrus wilsoni,* F:A.M. 34202 ("Sheep Creek")
 3. *Merycochoerus proprius,* F:A.M. 42469C (Upper Marsland)
 4. *M. matthewi,* F:A.M. 33317 (Lower Marsland)
2. Ticholeptinae:
 5. *Ustatochoerus major,* F:A.M. 34221 (Middle Ash Hollow)
 6. *U. medius,* F:A.M. 43030A (Valentine)
 7. *Ticholeptus hypsodus,* F:A.M. 43044 ("Lower Snake Creek")
 8. *T. tooheyi,* U.N.S.M. 1-15-9-36 ("Sheep Creek")
 9. *Mediochoerus blicki,* F:A.M. 43172 ("Lower Snake Creek")
 10. *M. johnsoni,* U.N.S.M. 2-11-8-36 (Upper Marsland)
3. Merychyinae
 11. *Merychyus (Metoreodon) relictus,* F:A.M. 43079 ("Lower Snake Creek")
 12. *M. (M.) relictus taylori,* F:A.M. 34319 ("Sheep Creek")

FIG. 49. Lateral and occlusal views of M^3:

3. Merychyinae (continued):
 13. *Merychyus elegans,* U.N.S.M. 2-10-8-30 (Upper Marsland)
 14. *M. crabilli,* F:A.M. 43391 (Harrison)
 15. *Paramerychyus harrisonensis,* F:A.M. 33314 (Harrison)
 16. *P. relictus,* A.M. 13813 (Harrison)
 17. *Oreodontoides oregonensis,* A.M. 7513 (= Harrison)
 18. *O. curtus,* A.M. 13817 (Harrison)
 19. *O. (Paroreodon) stocki,* A.M. 7814 (= Harrison)
4. Promerycochoerinae:
 20. *Promerycochoerus carrikeri,* F:A.M. 42312 (Harrison)
 21. *P. superbus,* A.M. 7445 (= Harrison)
 22. *P. (Parapromerycochoerus) barbouri,* F:A.M. 33315 (Harrison)
 23. *P. (P.) macrostegus,* A.M. 7450 (= Harrison)
 24. *P. (Pseudopromerycochoerus) minor,* C.M. 769 (Harrison)
 25. *P. (P.) montanus pinensis,* A.M. 12945 (Harrison)
 26. *Mesoreodon megalodon,* F:A.M. 33336 (Monroe Creek)
 27. *M. cheeki,* F:A.M. 33359 (Gering)
 28. *Promesoreodon scanloni,* F:A.M. 45354 rev. (Brule "D")

FIG. 50. Lateral and occlusal views of M^3:

4. Promerycochoerinae (continued):
 29. *Merycoides giganteus,* F:A.M. 33316 (Monroe Creek)
 30. *M. nebraskensis,* F:A.M. 33363 (Gering)
5. Phenacocoelinae:
 31. *Phenacocoelus stouti,* F:A.M. 44839 (Lower Marsland)
 32. *P. typus,* F:A.M. 33397 (Harrison)
 33. *Hypsiops brachymelis,* F:A.M. 34401 (Harrison)

34. *H. luskensis,* F:A.M. 44853A (Harrison)
35. *Submerycochoerus bannackensis,* F:A.M. 34317 (Harrison)
36. *Pseudomesoreodon rooneyi,* F:A.M. 44948A (Harrison)
37. *P. rolli,* F:A.M. 34481 (Harrison)

6. Desmatochoerinae:
38. *Megoreodon fricki,* F:A.M. 33308 (Monroe Creek)
39. *M. grandis loomisi,* F:A.M. 42321 (Gering)
40. *Desmatochoerus curvidens gregoryi,* F:-A.M. 37211 (Harrison)

FIG. 51. Lateral and occlusal views of M^3:

6. Desmatochoerinae (continued):
41. *Desmatochoerus hatcheri geringensis,* F:-A.M. 43316 (Gering)
42. *D.* (*Paradesmatochoerus*) *sanfordi,* F:A.M. 49636 (Gering)
43. *D.* (*P.*) *wyomingensis,* F:A.M. 37571 (Gering)
44. *Pseudodesmatochoerus wascoensis,* A.M. 7827 (= Harrison)
45. *P. hoffmani,* F:A.M. 45456 rev. (Monroe Creek)
46. *Superdesmatochoerus lulli,* A.M. 7469 (= Harrison)
47. *Subdesmatochoerus shannonensis,* F:A.M. 49550 (Brule "D")
48. *S. socialis,* F:A.M. 45177 (Brule "B")
49. *Prodesmatochoerus meekae,* F:A.M. 49549 (Brule "A")

7. Miniochoerinae:
50. *Miniochoerus cheyennensis,* A.M. 9797 (Brule "D")
51. *M. battlecreekensis,* U.N.S.M. 28044 (Brule "A")
52. *M.* (*Paraminiochoerus*) *ottensi,* F:A.M. 49546 (Brule "C")
53. *M.* (*P.*) *gracilis,* U.N.S.M. 28140 (Brule "A")
54. *Platyochoerus hatcreekensis,* U.N.S.M. 28511 (Brule "C")
55. *P. Platycephalus,* F:A.M. 45089 (Brule "A")
56. *Stenopsochoerus berardae,* F:A.M. 49617 (Brule "C")
57. *S. sternbergi,* F:A.M. 44980 (Brule "A")
58. *S.* (*Pseudostenopsochoerus*) *chadronensis,* geol. var., F:A.M. 45489 (Brule "A")
59. *S.* (*P.*) *reideri,* F:A.M. 49620 (Chadron "C")
60. *Parastenopsochoerus conversensis,* F:A.M. 45011 (Brule "A")

8. Oreonetinae:
61. *Bathygenys alpha,* F:A.M. 45334 (Chadron "B")
62. *Limnenetes playtyceps,* A.M. 9729 (Chadron "B")
63. *Oreonetes anceps,* C.M. 745 (Chadron "B")

9. Merycoidodontinae:
64. *Merycoidodon culbertsonii,* F:A.M. 45159 (Brule "A")
65. *M. forsythae,* F:A.M. 72303 (Chadron "B")
66. *M.* (*Anomerycoidodon*) *lambi,* F:A.M. 72139 (Brule "D")
67. *M.* (*A.*) *dani,* F:A.M. 72132 (Brule "B")

FIG. 52. Lateral and occlusal views of M^3:

9. Merycoidodontinae (continued)
68. *Merycoidodon* (*Blickohyus*) *lynchi,* F:A.M. 45297 (Brule "D")
69. *M.* (*B.*) *galushai,* R:A.M. 45279 (Brule "C")
70. *Paramerycoidodon georgei,* F:A.M. 45143 (Brule "A")
71. *P.* (*Barbourochoerus*) *major,* A.M. 1038, (Brule "D")
72. *P.* (*B.*) *bacai,* U.N.S.M. 28191 (Brule "B")
73. *P.* (*Gregoryochoerus*) *meagherensis,* F: A.M. 45462 (Gering)
74. *P.* (*G.*) *wanlessi,* F:A.M. 72109 (Brule "D")
75. *Otionohyus wardi,* F:A.M. 45015 (Brule "A")
76. *O. w. degrooti,* F:A.M. 49760 (Chadron "C")
77. *O.* (*Otarohyus*) *alexi,* F:A.M. 72060 (Brule "D")
78. *O.* (*O.*) *bullatus,* F:A.M. 45267 (Brule "B")
79. *Genetochoerus periculorum,* A.M. 6397 (Brule "A")
80. *G.* (*Osbornohyus*) *dickinsonensis,* C.M. 1584 (Brule "D")
81. *G.* (*O.*) *norbeckensis,* F:A.M. 49733 (Brule "B")
82. *Pseudogenetochoerus covensis,* C.I.T. 2688 (= Harrison in age)
83. *P. condoni,* A.M. 7881 (= Harrison in age)
84. *Epigenetochoerus parvus,* Y.P.M. 12420 (= Harrison in age)

10. Eporeodontinae:
85. *E. davisi,* A.M. 7622 (= Harrison in age)
86. *E. occidentalis,* Y.P.M. 10142 (= Harrison in age)
87. *E.* (*Paraeporeodon*) *longifrons,* A.M. 7567 (= Harrison in age)
88. *E.* (*P.*) *pacificus,* A.M. 7777 (= Harrison in age)
89. *Dayohyus trigonocephalus,* A.M. 7693 (= Harrison in age)

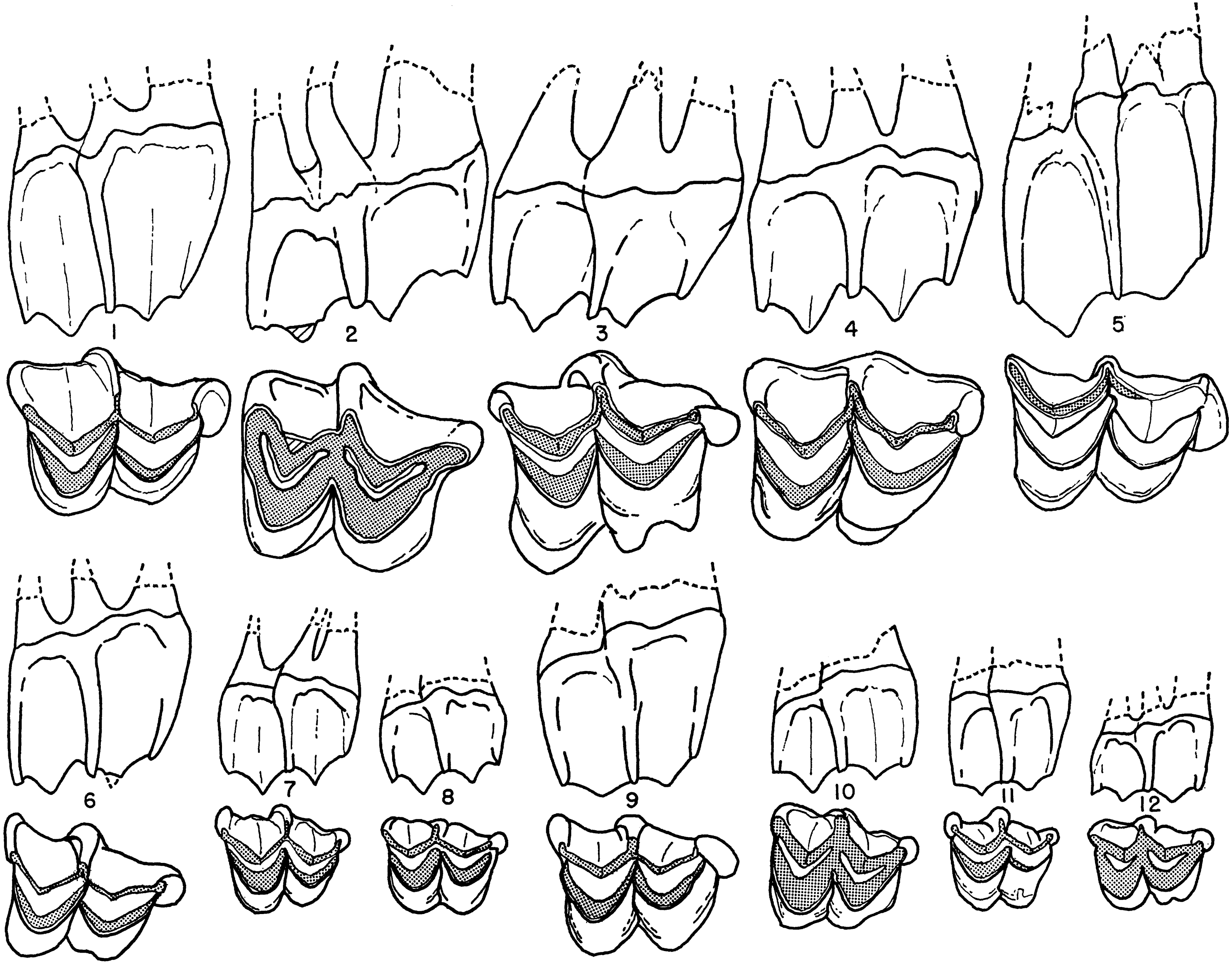


FIG. 48. Lateral and occlusal views of M^3: 1–4, Merycochoerinae, subfamily 1. 5–10. Ticholeptinae, subfamily 2. 11, 12. Merychyinae (in part), subfamily 3. (See chart 14, p. 416.) ×1.

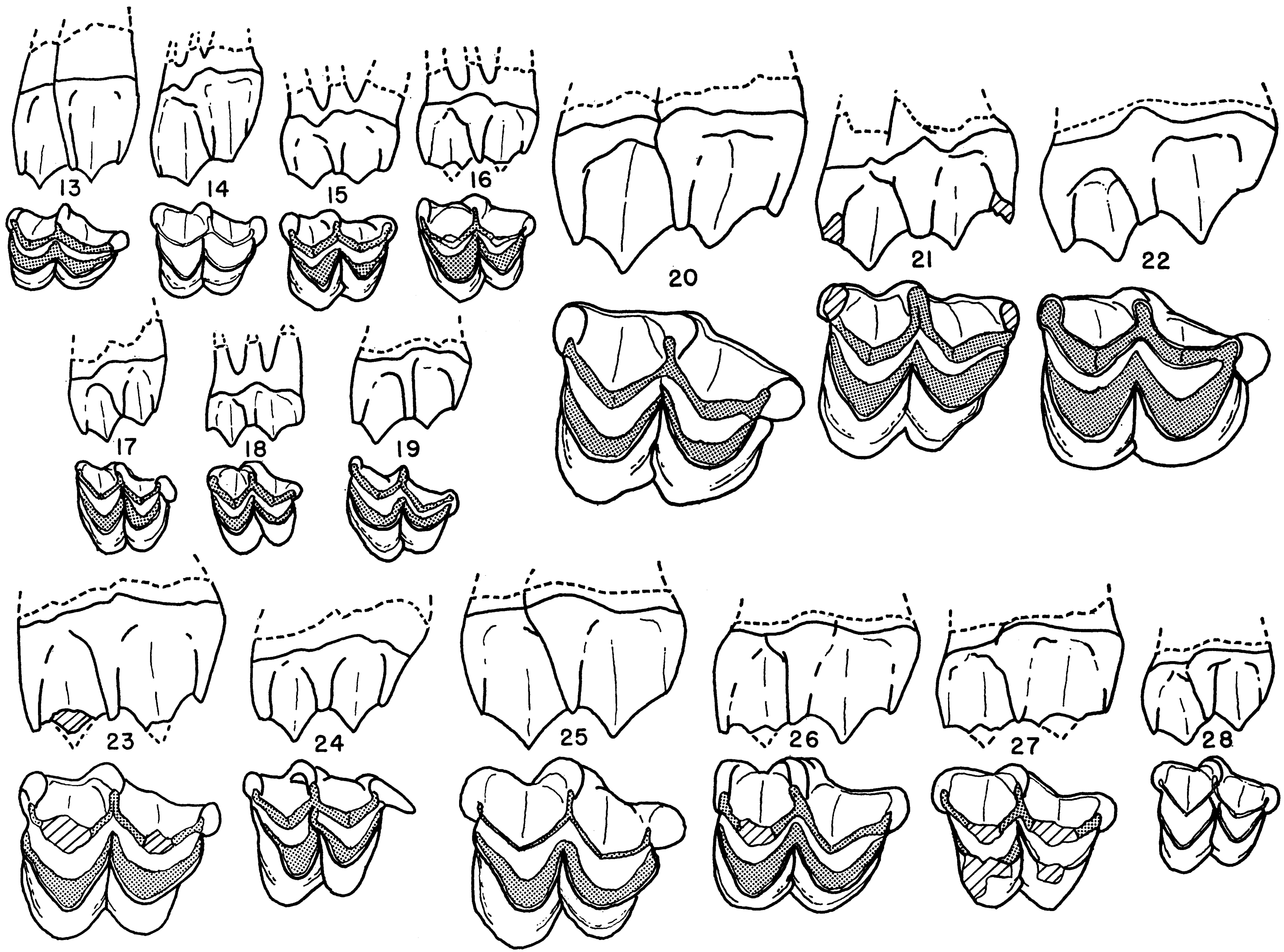


FIG. 49. Lateral and occlusal views of M^3: 13–19. Merychyinae (continued), subfamily 3. 20–28. Promerycochoerinae (in part), subfamily 4. (See chart 14, p. 416.) $\times 1$.

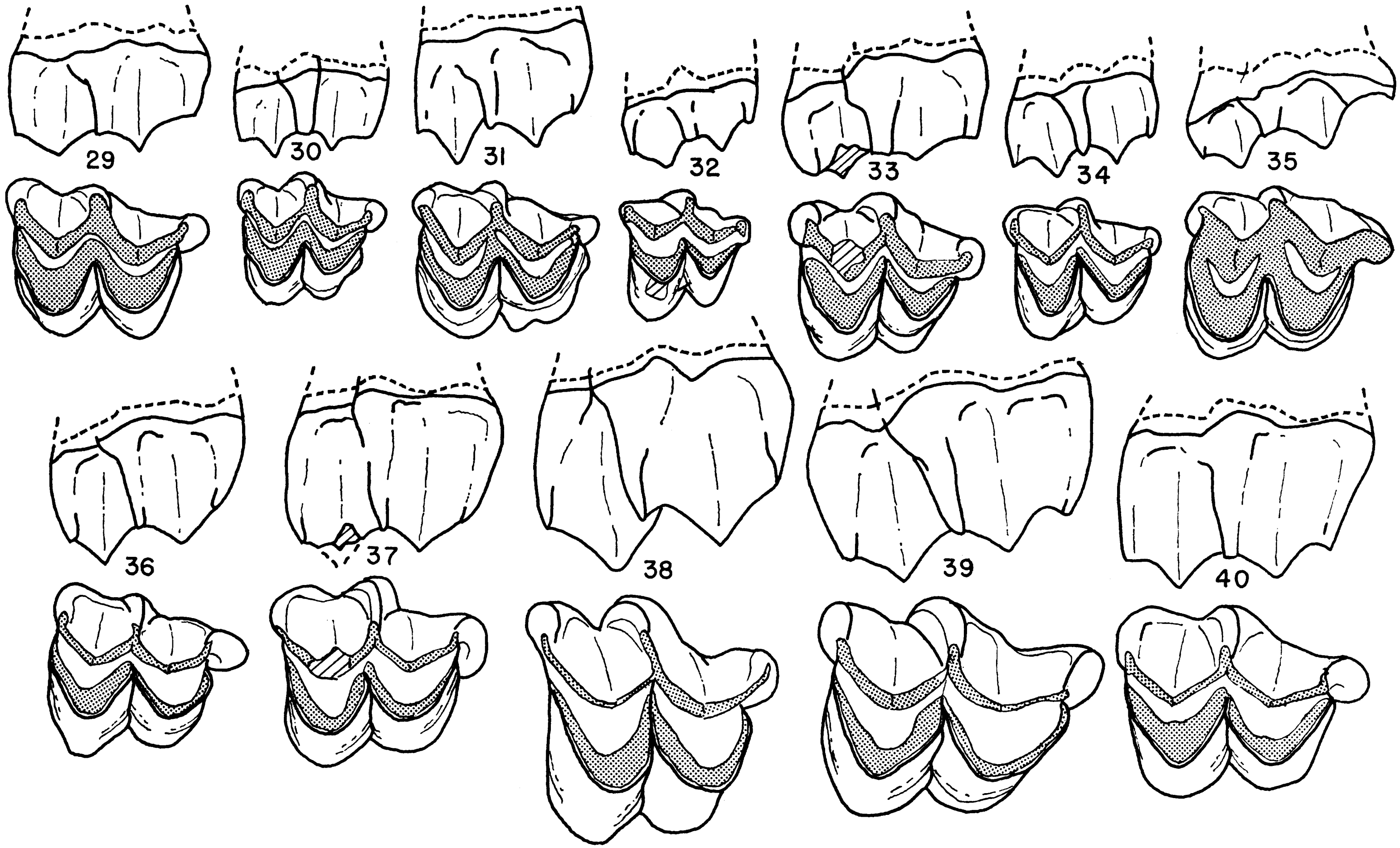


FIG. 50. Lateral and occlusal views of M^3: 29, 30. Promerycochoerinae (continued), subfamily 4. 31–37. Phenacocoelinae, subfamily 5. 38–40. Desmatochoerinae (in part), subfamily 6. (See chart 14, p. 416.) ×1.

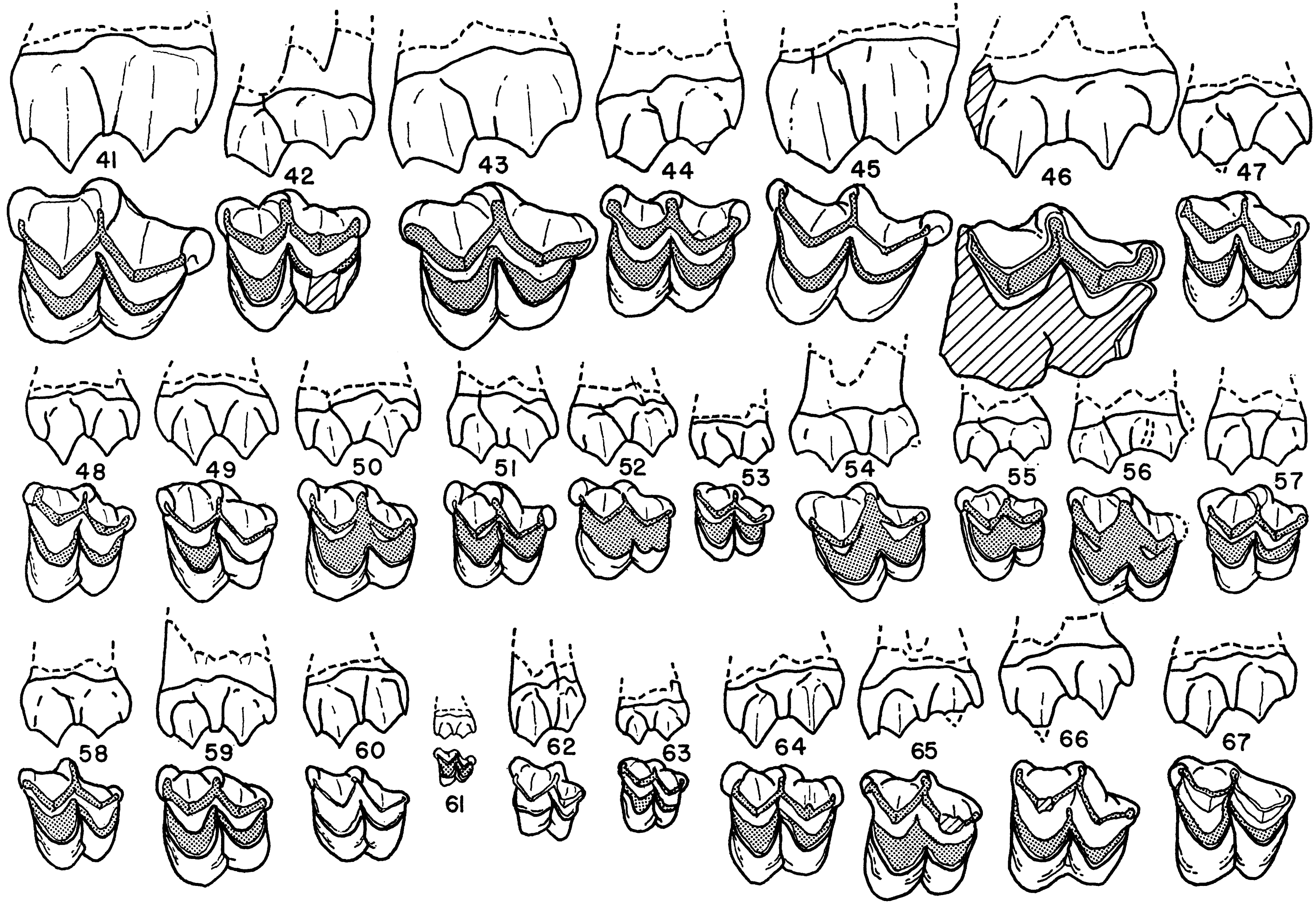


FIG. 51. Lateral and occlusal views of M^3: 41–49. Desmatochoerinae (continued), subfamily 6. 50–60. Miniochoerinae, subfamily 7. 61–63. Oreonetinae, subfamily 8. 64–67. Merycoidodontinae (in part), subfamily 9. (See chart 14, p. 416.) ×1.

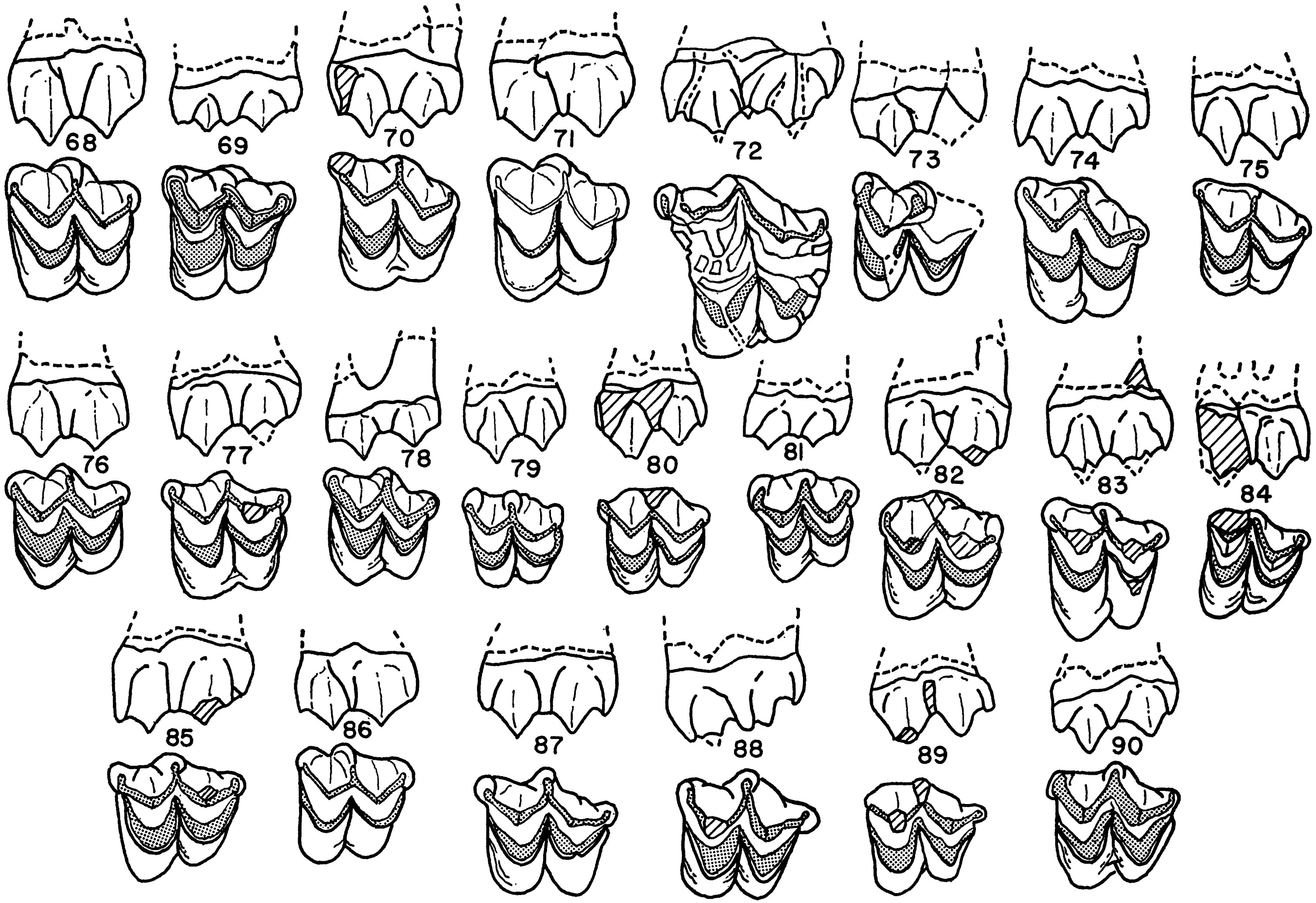


FIG. 52. Lateral and occlusal views of M^3: 68–84. Merycoidodontinae, subfamily 9. 85–90. Eporeodontinae, subfamily 10. (See chart 14, p. 416.) ×1.

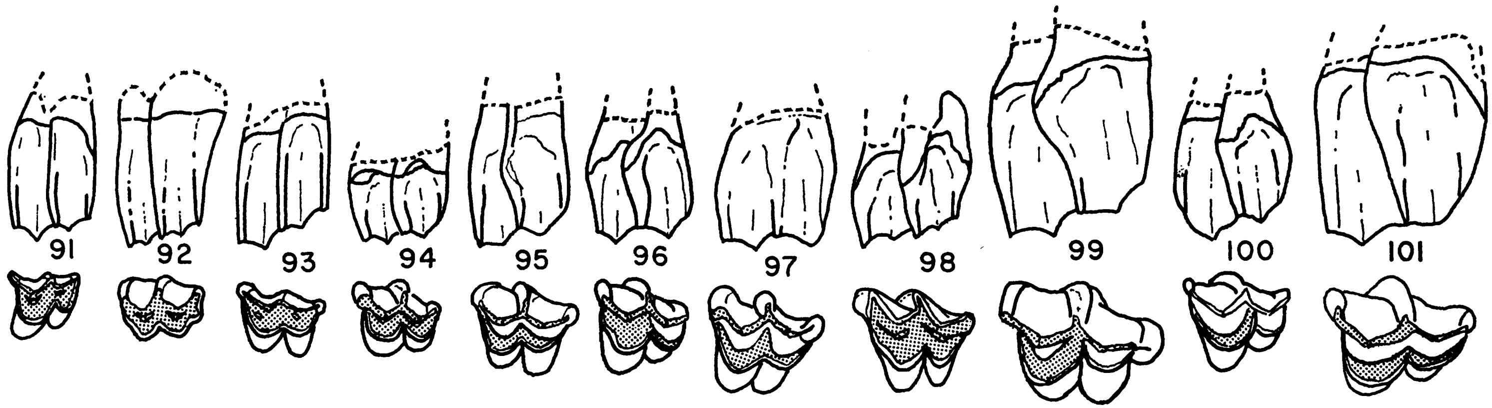


FIG. 53. Lateral and occlusal views of M^3: 91–101. Leptaucheniinae, subfamily 11. (See chart 14, p. 416.) ×1.

90. *D. wortmani,* U.C. 1911 (= Harrison in age)

FIG. 53. Lateral and occlusal views of M^3:
11. Leptaucheniinae:
91. *Sespia marianae,* U.N.S.M. 28448 (Lower Gering)
92. *S. ultima,* F:A.M. 45625 (Monroe Creek)
93. *Megasespia middleswarti,* U.N.S.M. 28408 (Upper Gering)
94. *Pithecistes tanneri,* U.N.S.M. 28492 (Brule "D")
95. *P. copei,* F:A.M. 56733 (Monroe Creek)
96. *Leptauchenia decora,* F:A.M. 45503 (Brule "D")
97. *L. margeryae,* F:A.M. 45632 (Monroe Creek)
98. *Hadroleptauchenia primitiva,* F:A.M. 45577 (Brule "D")
99. *H. densa,* F:A.M. 56901A (Upper Gering)
100. *Pseudocyclopidius frankforteri,* F:A.M. 45554 (Brule "D")
101. *P. lullianus expiratus,* F:A.M. 45601 (Monroe Creek)

TAXONOMY

SUBFAMILY: A subfamily in the oreodonts may include several genera and subgenera represented by specimens having certain outstanding morphologic characters in common. In a broad sense, all forms included in a subfamily are closely related.

Chart 21 lists various characters that are common to oreodonts in certain subfamilies. Some of these important morphologic characters, which do indicate a subfamily grouping, are: fan-shaped occipital region in the Merycochoerinae[1] and Miniochoerinae[2]; supraoccipital wings produced posteriorly beyond the condyles as in the Promerycochoerinae[3] and Merycoidodontinae[4]; molars with thin enamel and shallow fossettes such as are found in the Miniochoerinae[5] and Leptaucheniinae.[6] Thus it is evident that the same important character may be found in two different subfamilies. In the Leptaucheniinae and Miniochoerinae the dentitions are similar (thin enamel and shallow molar fossettes), but the shapes of the nasal bones differ widely. The Leptaucheniinae are recorded from oreodont faunal "Zone A" of the Brule through the Monroe Creek Formation, and examples of the Miniochoerinae, from faunal "Zone C" of the Chadron through "Zone D" of the Brule.

[1] Schultz and Falkenbach, 1940.
[2] Schultz and Falkenbach, 1956.
[3] Schultz and Falkenbach, 1949.
[4] Present report.
[5] Schultz and Falkenbach, 1956.
[6] Present report.

At present, the evidence is not sufficient for establishing definite relationships among all 11 subfamilies of oreodonts. The subfamilies, however, appear to be related to one another and thus had Eocene ancestors in common (see chart 14). More research work must be done in connection with the Eocene agriochoerids. Some subfamilies appear to have only one main phylogenetic line (such as the Merycochoerinae and the Merychyinae), but in other subfamilies several distinct lines parallel one another (such as the Leptaucheniinae and the Merycoidodontinae). The rate of development in the various parallel lines within a single subfamily was not the same.

In establishing a subfamily, the writers have examined the characters common to all genera and have reviewed the geologic occurrence of each. A consideration of the geologic distribution of the forms representing each phylum in a proposed subfamily has been found to be essential in taxonomic studies.

GENUS AND SUBGENUS: A genus (or subgenus) in the Merycoidodontidae usually embraces a group of species that are from different geologic faunal zones but within a vertical phylum. All species in a phylum have the morphologic characters of the subfamily and genus.

The difference between a genus and a subgenus may be chiefly that of size; i.e., the specimens representing the subgenus may possess morphologic characters that differ only slightly from those of the genus, but may be considerably smaller or larger. This size difference would be greater than that in the expected sex variation, and the size ratio may persist through several geologic faunal zones. This is evident in the Desmatochoerinae with the two phylogenetic lines *Desmatochoerus*[7] (the larger) and *D.* (*Paradesmatochoerus*)[8] (the smaller).

Two genera may differ essentially in only one important character. A very prominent sagittal crest is present in *Desmatochoerus*[9] but is lacking in *Pseudodesmatochoerus.*[10]

[7] Schultz and Falkenbach, 1954, p. 177.
[8] Schultz and Falkenbach, 1954, p. 193.
[9] Schultz and Falkenbach, 1954, p. 177.
[10] Schultz and Falkenbach, 1954, p. 203.

When several genera and subgenera are considered so closely related that they are included in one subfamily, the early stages of each phylum are not always readily recognized. Such is essentially true of certain oreodont lines in the Merycoidodontinae which diverged from the main stock during late Chadron and early Brule times. In these instances, the later members of a generic or subgeneric line may have evolved so as to indicate apparent morphologic differences, which may be only minute in earlier forms of the same lines.

A genus and a subgenus show close affinities to each other and, where possible, the first-occurring line or the longest (geologically) has been given generic rank. The subgenus is used to show close relationship and may be earlier, later (geologically), or contemporaneous with the genus.

A genus (or subgenus) has been established when a phylum appears to extend vertically through at least two geologic periods of a sequence. The occurrence of more than one species of a genus in a faunal zone usually indicates another phylum, which was just beginning to split off from the primary phylum. However, a species that is recognized only in one faunal zone has been considered as a member of the closest genus or subgenus. Examples are obvious in *Megoreodon*, i.e., M. *grandis loomisi*, geologic variety,[1] a large form from the Monroe Creek deposits, and the smaller (perhaps dwarf) form, *M. fricki*,[2] from the same area and age. If a small *Megoreodon*-like species had occurred in the Harrison deposits and evidence indicated that it had evolved from *M. fricki*, the two species would have been considered subgenerically different from *Megoreodon*.

In the genus *Brachycrus*,[3] it would appear that independent phylogenetic development took place in widely separated areas, namely, in the central Great Plains, in the Rocky Mountain area to the west of the Plains, and perhaps in the northern Great Plains and California. At least there is morphologic evidence to substantiate this in *Brachycrus* material from the "Sheep Creek" and "Lower Snake Creek" deposits of Nebraska, from upper Miocene sediments of the Devil's Gate area of Wyoming, and from upper Miocene deposits in Montana and California. No doubt these represent several phyla, but it seemed unreasonable to establish three or four subgenera, as the differences are slight and perhaps are due to the evolution of the forms in their own local environments. The generic (or subgeneric) rank is of much importance in the oreodonts. The apparent morphologic changes in forms in a generic (or subgeneric) phylum from one faunal zone to the next are often slight: perhaps the differences relate chiefly to changes in size, so that the specific rank may be of little value.

The present writers realize that the criteria for a genus in one family may not be exactly the same as in another. In fact, the basis for a genus (or subgenus) within the oreodonts in general is not always precisely the same but only approximate. The most important factor is that the generic phylum be a vertical one.

SPECIES AND SUBSPECIES: A specific or subspecific name in the oreodonts embraces all examples that are referable to that particular form, not the holotype alone. These examples are usually confined to a given geologic faunal zone. In a specific or subspecific group, four kinds of variation must be considered: (1) individual; (2) sexual (if observable); (3) geographic; and (4) geologic. The last two may be comparable. Geographic variation may have been the result of the migration of some representatives of a species to areas with slightly different environmental conditions from those that had existed in their former dwelling place. Geologic variation may represent morphologic changes which are apparent at a higher or lower geologic level within the same general faunal zone. (These differences are discussed on p. 401.)

A species (or subspecies) is distinguished by its own morphologic characteristics from other species in a generic lineage. In the comparatively more slowly evolving lines, the difference between species from the various faunal zones is chiefly a matter of size, the later forms usually being the larger. Other characteristic differences may be only slight. In *Merycoidodon* (*Anomerycoidodon*), size change is not great, but the change in the bulla from minute to greatly in-

[1] Schultz and Falkenbach, 1954, p. 174.
[2] Schultz and Falkenbach, 1954, p. 167.
[3] Schultz and Falkenbach, 1940, Merycochoerinae.

flated, and the varying prominence of the hyoidal groove on the bulla, are both diagnostic.

The Merycoidodontinae species from the Chadron, and oreodont faunal "Zone A" of the Brule, all possess small (minute) bullae. Those from faunal zones "B," "C," and "D" of the Brule have inflated bullae. The change from small (minute) to inflated is abrupt, owing to the fact that there is a break in the stratigraphic sequence, and no fossils have been found that would represent the hiatus. No evidence of the transforming from minute to inflated has been observed. Perhaps fossiliferous sediments representing the period of time of the hiatus will be discovered. (See discussion, p. 402.)

A true sequence could be established if fossils could be obtained from each vertical foot of the deposits of the Tertiary, with no faunal breaks. This would not only eliminate subgenera in a direct vertical sequence but perhaps also the species (or subspecies). The net results would be a generic (vertical) phylum.

The holotype of a species, when chosen by the present writers, has been as complete a specimen as possible, as well as being an average example of the specific assemblage.

A subspecies is used in three ways: (1) as a morphologic variant; (2) as a geographic variant (when separated by great geographic distance); and (3) as a geologic variant (when a species occurs in two different faunal zones of the geologic sequence without much apparent change). The writers believe that it is as important to point out a lack of change in a form occurring in a geologic sequence as it is to demonstrate progressive development. The subspecies usage here actually indicates that examples of a species differ somewhat from the average examples of the species, and the said differences may be attributed to one of the three mentioned subspecific variations.

The use of the term "subspecies" for living mammals differs considerably from the average use of "paleosubspecies." The present writers believe that, in general, a paleospecies is approximately equal to a subspecies of living mammals, and that a paleosubspecies is more or less equal to a recent variety.

Stirton,[1] at variance with the above, stated, "It is true that a great number of our so-called species still listed in the fossil record will eventually be recognized as genera; . . ." Stirton further discussed species and subspecies, using horses as a basis to justify his beliefs. The present writers do not wish to imply knowledge of the horse, but rather to say that the extent of research on the horses was preliminary work. Stirton's statement (p. 29), "Adequate samples of complete crania are seldom found," is only partially true. The Merycoidodontidae remains are represented by many fine associated skulls, mandibular rami, and skeletal elements. The evaluation, especially specific and subspecific, of well-preserved skulls certainly will necessitate a different criterion of characters from that of dentition alone.

Stirton (p. 32) also reported, in a discussion concerning dentitions: "I can exemplify this best with two closely related species of the equid genus *Neohipparion, N. floresi* . . . and *N. arellanoi* . . . from the middle Pliocene Boquilla formation in the Rio Papigochic Valley, Chihuahua, Mexico. . . . All are middle Pliocene, and are among the more progressive species of the genus. A large number of maxillary and mandibular cheek teeth series, isolated cheek teeth, and metapodials were available. The species were not found in the same assemblages or localities but one species was found in 3 localities and the other in 3 different localities. It is interesting to note, however, that Mr. Lloyd C. Pray's studies on the stratigraphy offer no basis for a time difference between the assemblages from these localities. . . .

"Though there is a variation in the crown height in different individuals, *N. arellanoi* seems to average from 5 to 10 mm. lower crowned than *N. floresi.* This character is only suggestive."

This conclusion is followed by a detailed discussion of the crowns of the two mentioned species. Stirton further stated (p. 36): "A survey of all the features in the teeth and in the metapodials of *N. floresi,* and *N. arellanoi,* indicates a remarkably close relationship. Since there is an intergradation of varying degree in seven of the nine diagnostic characters, these forms might be interpreted as representing successive subspecies in a chronocline. Though characters are not necessarily of equivalent value in different species or subspecies, nevertheless, when similar dental features are com-

[1] 1955, pp. 26-37.

pared in the horse, the ass, and the zebras, it is felt that the characters displayed in the Papigochic neohipparions are of at least equivalent if not of greater magnitude than in the living equids."

In summation: (1) if the ages of the deposits from which the samples in question occurred are the same, there are two species of a single genus living at the same time in the same valley; (2) if successive subspecies are suggested by the characters of the teeth, it is without geologic support; (3) if the first instance is correct, perhaps two phylogenetic lines are represented, possibly a genus and also a subgenus.

As previously noted in the Merycoidodontidae, the writers are fortunate in having an abundance of complete material to evaluate the morphologic characters and not depend upon the dentition alone. As in (3) above, possibly the skulls of the two species are considerably different, although the dentitions are somewhat similar. In the oreodonts it would be impossible, with few exceptions, to establish species, or genera, without the skull characters plus the geologic data. One would expect that horse skulls have characters of value in addition to dentitions. If the oreodonts were considered from the dentitions alone, the "evidence" would suggest quite different conclusions.

The height of a horse tooth may well be diagnostic of its geologic occurrence. However, in the Merycoidodontidae this particular character is valueless from a stratigraphic approach. As noted elsewhere, the dentition of examples of *Sespia* are comparably more hypsodont than that of the modern horse—yet examples of *Sespia* are not known later than the Monroe Creek Formation. However, larger-skulled forms with semibrachyodont teeth lived until mid-Pliocene.

An evalution of any taxonomic rank within the oreodonts cannot be reached until one knows the morphologic and geologic history of the available examples of a phylogenetic line. Then it is possible to arrive at a generic, subgeneric, specific, subspecific, and varietal classification. Unfortunately there is not a standard for a definition of a species in vertebrate paleontology. A species of one worker may be a genus of another, or perhaps even a subspecies. Also, another worker may attribute the same morphologic differences under consideration to individual variation within a single species or subspecies.

Stirton's discussion was of a subspecies, and he placed great importance on its rank. The present writers place little emphasis on a subspecies except for its variation from the species in minor characters.

Use of Terms "Primitive" and "Specialized"

The present authors have tried to avoid the use of the terms "primitive" or "specialized" for characters in the description or text for any taxonomic rank, but consider these useful terms. In the oreodonts a character may be primitive or specialized in any single phylogenetic line, but the same character cannot be designated as primitive or specialized when the family as a whole is considered, nor is a character that is thought to be specialized in one phylum necessarily so regarded in another. George Gaylord Simpson[1] ably defined the two terms in the following manner: "The concepts of primitive and specialized are relative and are meaningless unless definitely related to a particular taxon, lineage, or phylogeny. Within a taxon, the characteristics of the common ancestry are primitive and others are more or less specialized in proportion to their departure from the ancestral condition. Within a single lineage, characteristics occurring earlier are more or less primitive and those appearing later more or less specialized in proportion to their times of appearance. Within a phylogeny (which is divided into taxa and consists of branching lineages) characteristics of any one common stem are more primitive than different characteristics of its descendant branches; within single branches they are more specialized in accordance with earlier or later appearance; and between branches they are more primitive or more specialized in accordance with less or more departure from the stem condition."

The small (minute) bulla is considered a primitive character in the subfamily Merycoidodontinae, in which the earliest forms had the minute bullae that evolved into inflated ones in the later geologic faunal zones. However, in the Miniochoerinae, the bulla remained minute

[1] 1961, p. 99.

throughout the subfamily history. In the latter instance, in a strict sense this character may not be considered as a primitive one within the subfamily. In the Oreonetinae from "Zone B" of the Chadron, one of the earliest known subfamilies, the bulla is inflated and completely round, similar to examples of Merycoidodontinae from "Zone D" of the Brule. In the development of the Oreonetinae, the inflated bulla remained nearly static and cannot be considered either primitive or specialized. If the ancestral forms that gave rise to the Oreonetinae had minute bullae, this character would be considered a primitive one.

In the Merycoidodontinae, several phyla indicate that the lacrimal fossa becomes shallower as the forms occur higher in the geologic section, a character that would be considered specialized for these particular lines. In the Desmatochoerinae, the lacrimal fossa continues to be moderately deep, and throughout the geologic history of the subfamily no change is apparent in this particular character.

Enormous change or development in the nasals is apparent throughout the family. In *Brachycrus* the nasals are extremely specialized even when compared with those of *Merycochoerus* which are also retracted and shortened. In the leptauchenins no anterior reduction has occurred, but the nasal bone is a narrow bar extending from the frontal to above the superior canine, then widening to join the maxilla. The narrowness of the nasal bones is due to the large nasal-facial vacuities of the subfamily. All examples of the Leptaucheniinae have similar nasal areas; therefore this character should not be considered specialized or primitive.

The first perceptible anterior nasal retraction occurred in the Phenacocoelinae from the Harrison Formation or deposits approximately equal in age. The most noticeable nasal reduction in this subfamily is in the genus *Submerycochoerus,* which apparently gave rise to *Merycochoerus* (from the Marsland Formation). The line demonstrates a graduated reduction of the nasal length through the geologic sequence. Certainly the nasals of *Submerycochoerus* demonstrate a much more primitive character than do those of *Merycochoerus.*

In the Ticholeptinae, the foreshortening of the nasal also is noticeable. Examples of *Ticholeptus* from the upper Miocene show some reduction in nasal length, whereas those of *Ustatochoerus* from the lower and middle Pliocene show a graduated reduction. The nasal area of *Ticholeptus* is more primitive than that in *Ustatochoerus.*

The reduction in nasal length is definitely a trend in various phylogenetic lines. Although it is a specialized character in different phyla, the reduction of the nasals in the various lines occurs at different geologic times.

The occipital regions are divided into two forms on the basis of shape: (1) supraoccipital wings that are narrowly spread and produced posteriorly beyond the condyles; and (2) widely spread wings that are incorporated into a fan-shaped occipital region.

The Desmatochoerinae and Merycoidodontinae have the posteriorly produced supraoccipital wings. The former subfamily has the longest geologic range of any of the subfamilies of oreodonts from oreodont faunal "Zone C" of the Chadron Formation to the upper part of the lower Harrison Formation (Oligocene–lower Miocene). The latter group extends from oreodont faunal "Zone B" of the Chadron Formation to the Gering (lower Oligocene to lower Miocene), and gave rise to the Promeryochoerinae, which ranged through the Gering, Monroe Creek, and Harrison formations (lower Miocene). All these subfamilies retained the posteriorly produced occipital region. The fan-shaped occipital region has a more extended geologic history. It is observed in: the Oreonetinae from oreodont faunal "Zone B" of the Chadron Formation; the Miniochoerinae from "Zone C" of the Chadron and from all four oreodont faunal zones of the Brule Formation; the leptauchenins from the Brule, Gering, and Monroe Creek formations; and the Merychyinae from the Harrison, Marsland, and Sheep Creek (= "Sheep Creek" and "Lower Snake Creek"), Valentine, and lower and middle Ash Hollow formations. In the Merychyinae the fan-shaped occipital region is primitive in examples from the Harrison compared with those of the Sheep Creek (= "Sheep Creek" and "Lower Snake Creek") Formation.

The dental series vary in many aspects: usually the teeth are brachyodont, but some are hypsodont; some lack external superior molar styles; a few examples have internal styles on molars similar to those of the cervids (the latter character is not considered diagnostic); and others have crowns covered with thin enamel and have shallow molar fossettes. These various characters are primarily considered at the subfamily level, but they influence decisions down to the subspecies level.

The extremely long-crowned molars of the tribe Sespiini (subfamily Leptaucheniinae) are more hypsodont than in any other subfamily of oreodonts. As mentioned elswhere, the molars of *Sespia* from the Monroe Creek Formation (lower Miocene) are comparatively more hypsodont than those of the recent horse (see fig. 42, present paper).

The remains of the Sespiini and those of the Leptaucheniini are here considered under one subfamily; the skulls are similar in general characters, even to the unique nasal-facial vacuities known only in the Leptaucheniinae. The skulls of the Sespiini approach the size of the smaller examples of the Leptaucheniini, but the molars are definitely much more hypsodont than in the latter tribe. Both tribes apparently had a common ancestor, but it is difficult to determine the time when they branched into two groups. The Sespiini are not known from Oligocene deposits, and the earliest known Miocene forms are very distinct from the Leptaucheniini. There was a tendency in the Leptaucheniini also to develop hypsodont teeth, but this process of evolution was slow and the group became extinct before extreme hypsodonty was attained. Hypsodont teeth are a specialized character in this subfamily.

Examples of the Miniochoerinae, Leptaucheniinae, and the Merycoidodontinae were all more or less contemporaneous, yet the dentitions of the last subfamily are diagnostically different from those of the first two. In dental examples of the Merycoidodontinae, the crowns are covered with comparatively heavy enamel, and the molar fossettes are deep, as is also true of all the other subfamilies with the exception of examples of Miniochoerinae and Leptaucheniinae. In these subfamilies, the tooth crowns had a covering of thin enamel which was lost with slight wear, and the molar fossettes were shallow. There is no apparent close relationship between the Miniochoerinae and the Leptaucheniinae, yet the teeth of both groups were quite similar and were in apparent static state of development. Apparently the teeth were "specialized," but more examples of early Oligocene dentitions are needed to determine when this specialization took place.

The five-digit forefoot is the one possible true primitive character that may be credited to the entire family. The presence of a five-toed forefoot has been observed in several different subfamilies of oreodonts. It is reasonable to suspect that all early oreodonts had five digits on the forefoot and that this was a primitive character preserved in some species occurring in the Oligocene and lower Miocene.

HOLOTYPE: The present writers have not disagreed with previous authors as to the various specific holotypes. In several instances, a lectotype has been selected from a syntypic series.

The problem of determining the holotype of *Promerycochoerus superbus* (Leidy) is somewhat complicated. The specimen is also the genoholotype. Leidy's original description was based on several individuals. Douglass[1] quoted Leidy's original description in part, "The species, which I propose to distinguish under the name *Oreodon superbus,* is indicated by a mutilated skull, together with mutilated crania and portions of jaws." Douglass then stated, "what we should undoubtedly consider as the type of this species is the skull represented in Fig. I, Pl. I, of Leidy's Extinct Vertebrae Fauna." This is also the skull considered as the "example" in the present revision. The present writers agree with various earlier workers[2] that the skull and mandible, A.M. 7431, is typical of *P. superbus.* This skull and mandible are well preserved and have been considered as *Promerycochoerus.* As *P. superbus* is the genotypic species, the present writers believe that the specimen in question should continue to be the generic "example," even if the mutilated skull should be found and proved to differ specifically from A.M. 7431.

In the synonymizing of *Pronomotherium* with *Brachycrus,* the circumstances were different from those in the above situation. Both generic names were given to the same kind (generic) of specimens. *Brachycrus* Matthew

[1] Douglass, 1907b, p. 87.

[2] Cope, 1888, pl. 26, fig. 2; Scott, 1890b, pl. 14, fig. 10; Zittel and Schlosser, 1911, fig. 675b; Zittel and Schlosser, 1923, fig. 716b; Schultz and Falkenbach, 1949, p. 108, figs. 2-5, 11, and 12.

has priority and should be the name used.

Merycoidodon, the first-named genus of the oreodonts, was based on fragmentary evidence. These fragments compare readily with several examples of various genera and subgenera in different phyla, all from the Brule Formation. We here again accept the consensus of what represents an example of *M. culbertsonii.*

Many of the early designated holotypes lack associated geologic information; in fact, some even lack geographic data. In some instances the original field labels have been found by the present writers, and these have helped to establish the general collecting areas. This information gave F:A.M. and U.N.S.M. field parties an opportunity to collect from the same areas. New material was discovered and compared with the types. When the examples were found to be specifically the same as the holotypes, and the degree and type of fossilization also were similar, it has been assumed that the original localities and geologic horizons were rediscovered. The writers realize this method may involve geologic errors, but the margins of mistake would be limited.

Variation in Individuals

Individual variation is perhaps best exemplified in *Merychyus crabilli.* In 1947[1] 10 associated specimens were listed according to individual age (external height of M^3) with the measurements of various parts, and were arranged to demonstrate the range in variation in each individual. Individual variation, in a strict sense, is apparent only in material that occurred at the same horizon, a quarry assemblage, or a "family group" such as *M. crabilli.* When material from another area, where there is no absolute geologic tie, or specimens from a different horizon are included in a study, geologic variation may well be present.

Sexual variation is not always apparent in the oreodonts. The most noticeable is in the genus *Ustatochoerus*[2] in which the male and female skull examples may have the same basal length, but the female example is noticeably narrower and lighter than that of the male. It is noteworthy that sexual variation is most conspicuous in the *Ustatochoerus* phylum, which is the last (geologically) known line of the oreodonts (from the Pliocene).

In *Promerycochoerus,*[3] the sexual variation is less noticeable than in the *Ustatochoerus* line. The male skull examples of *Promerycochoerus* are more robust and the zygomatic arches are massive in comparison with those of the females. In *Mesoreodon* (ancestral to *Promerycochoerus*) the sexual variation is less prominent than in *Promerycochoerus.*

In the Merycoidodontinae, especially in *Merycoidodon culbertsonii,* the remains show considerable individual variation. How much of this may be sexual variation is questionable. However, the end members of the various phyla suggest that skull examples of the males are wider and more robust than those of the female. It seems obvious that these examples of the same phyla, which occur lower in the geologic section, do not suggest sexual variation.

In two instances two skulls were found associated in the field. These four skulls have been referred to *M. culbertsonii osborni,* all from oreodont faunal "Zone A" of the Brule Formation of South Dakota and Wyoming.

Table 4 (p. 104) shows the various measurements of the two associated skulls (F:A.M. 45217A and 45217B) from South Dakota. The outstanding individual variations are the blunt posterior border of the nasals and the distantly placed supraorbital foramina in F:A.M. 45217A compared with the pointed nasal border and the closeness of the supraorbital foramina in F:A.M. 45217B. (See fig. 1.)

The cited percentage difference in a given measurement of the skulls is not so great as may be expected. Except for the distance between the supraorbital foramina, the greatest is 20 per cent, and that is between the width of P^1 on the left and P^1 on the right side of F:A.M. 45217B.

The two Wyoming skulls (F:A.M. 72246A and 72246B) are longer than the two South Dakota skulls but within the expected individual variation of a species or subspecies. It is of interest that the same variation of the posterior border of the nasals is also apparent in the two Wyoming skulls but to a lesser degree.

The degree of individual variation of the four skulls in question is less than would be expected, especially when it is realized that, in

[1] Schultz and Falkenbach, 1947, p. 262, charts 3 and 4.

[2] Schultz and Falkenbach, 1941, p. 11.

[3] Schultz and Falkenbach, 1949.

a comparison of specimens from South Dakota and Wyoming, some degree of geologic variation may be present, i.e., within oreodont faunal "Zone A" of the Brule.

Variations in Dentitions

The dentition of the Merycoidodontidae varies from brachyodont, especially in Oligocene forms, to extremely hypsodont in *Sespia* of the lower Miocene. The hypsodont or brachyodont dentition has no correlation with the geologic sequence. The most hypsodont examples, in the Sespiini, occur in the Monroe Creek Formation.

The breadth of the third molar varies in some phylogenetic lines—the higher the example occurs in the geologic sequence, the wider the tooth. (The anterior-posterior length may remain static or increase.) This variation is best exemplified in the Miniochoerinae.

In the Oligocene forms, the anterior and posterior crescents of the molars slope more internally than do those from the Miocene and Pliocene. This particular character may be correlated with the geologic sequence. This also coincides with the prominent faunal break between "Zone D" of the Brule and the Gering.

The formula is I^3_3, C^1_1, P^4_4, and M^3_3 with the exception of the leptauchenins which may vary in the incisors, I^{2-3}_3. The lower canine is incisiform, and P_1 is caniniform throughout the family. The superior premolars may or may not have anterior intermediate crests—a variation in genera and species. The external styles of the molars are almost absent from *Sespia* and vary in degree of prominence in other forms. The inferior premolars, including P_1, may or may not have posterior intermediate crests, varying in genera and species.

It is of interest that a varied group of mammals such as the oreodonts, which exhibit many changes in the skull characters, lacks any change in the formula of the premolars. The camels, as an example, have lost premolars, and the lengths of the diastema between the premolars vary. Functionally, the teeth of the Merycoidodontidae have remained the same.

Previously some stress has been applied to the fact that a P^4 may have one or two anterior pits. This characteristic depends strictly on the fact that P^4 may have an anterior intermediate crest and a valley or fossette on each side of the anterior crest. These are lost with brief wear and, therefore, are not of diagnostic value.

Throughout this revision of the family the terms "brachyodont" and "hypsodont" have been used. These have, however, been treated as terms for comparison within the Merycoidodontidae. With the exception of the Sespiini, which actually have very hypsodont molars, all other oreodonts have cheek teeth ranging from brachyodont to semihypsodont when compared with those of other mammals.

Many of the molar teeth possess cingula, but considerable individual variation is noted in this character. A study of the cingula on third upper molars suggests certain differences: (1) some examples of *Brachycrus wilsoni* have the cingula exposed (above the alveolar borders); (2) some examples of *B. siouense* have the cingula concealed (below the alveolar border), which suggests that *B. siouense*, with the concealed cingulum, had more hypsodont molars than *B. wilsoni*, with the exposed cingulum. Such is not the fact, however, since both forms have examples with the same ratio of the height of the external enamel to the anteroposterior length of the tooth.

A similarity has been noted in *Pseudomesoreodon* in that the cingula in examples of *P. rolli* are concealed and in those of *P. rooneyi* are exposed. In *Ustatochoerus, Ticholeptus, Mediochoerus, Merychyus, M.* (*Metoreodon*), and all genera of the Leptaucheniinae the cingula are concealed. In all other genera and subgenera of the oreodonts not noted above, the cingula appear to be exposed.

The value of this observation is questionable in that the age of the individual no doubt enters the problem. An aged individual, in many instances, has the cingulum exposed, yet a younger individual of the same form may have the cingulum concealed.

In *Ustatochoerus* from the Valentine and Ash Hollow formations, and the various genera of the Leptaucheniinae from the Brule, Gering, and Monroe Creek formations there is a concealed cingulum on M^3. Many more specimens should be examined and plotted as to age of the individual, specific variation (if any), and geologic occurrence.

The ratio of the height of the outside enamel to the anteroposterior length of M^3 is more or less static. It is of interest that skull examples of *Ustatochoerus medius* from the Valentine Formation are approximately 28 per cent smaller than those of *U. major* from the mid Ash Hollow, yet the ratio of the height to the anteroposterior length of the M^3 is about the same.

U. medius (Valentine)
F:A.M. 37226, AP/H of $M^3 = 96\%$
F:A.M. 34220, AP/H of $M^3 = 88\%$

U. major (Mid Ash Hollow)
F:A.M. 34221, AP/H of $M^3 = 97\%$
F:A.M. 34220, AP/H of $M^3 = 87\%$

These four examples show an 8 to 10 per cent variation within the species, but a 1 per cent difference in the maximum and minimum of the two species. Similar results are found in a comparison of examples of *Brachycrus rusticus* from the lower part of the sequence of the Sweetwater River area of Wyoming and those of *B. sweetwaterensis* from the upper portion of the same deposits.

In a similar comparison between phyla, some are approximately the same, and some obviously have a different ratio. Examples of *Sespia* are outstanding in having an extremely hypsodont M^3.

The anteroposterior length of a dental series (P^1–M^3) is affected to a small degree by the age of an individual, as is illustrated in the Merychyinae.[1] The third upper molar increases in anteroposterior length, but M^1 and M^2 decrease slightly, with wear, a situation that is essentially true in all oreodonts. The larger the tooth series, the more variation can be expected. In aged individuals (w‡‡ or better), however, both the premolars and molars series reduce in over-all length.

In remains of the Merychyinae[2] considerable variation has been noted. The *Merychyus* dentitions may possess either comparatively large or small canines, which may be associated with either comparatively large or small premolars. In *M.* (*Metoreodon*) all the canines are small. In the *Merychyus* assemblages one suspects that the large canines indicate male examples, but apparently such is not the case. That only small canines have been recorded for *M.* (*Metoreodon*) seems to indicate that the sizes of the canines and the premolar series cannot be used for probable sexual determinations.

Variation in Auditory Bullae

Considerable variation exists in the auditory bullae of the Merycoidodontidae. The change of the bullae is considered to be from small to large (see discussion, p. 403), and is best demonstrated in the Merycoidodontinae (p. 24) in which the forms of a given phylum from the Chadron and oreodont faunal "Zone A" of the Brule have minute bullae, and those from "Zone B" or higher in the same phylum have inflated ones. Of interest is the fact that, within the Brule, the "Zone B" forms of the Merycoidodontinae have inflated bullae but a noticeable groove for the hyoid; in "Zone C," the groove is less prominent; and from "Zone D" it is completely absent.

There also is considerable difference in the amount of inflation of the bulla, i.e., the skulls of two species of approximately the same size may both have inflated and rounded bullae, but one form has proportionately larger bullae than the other. This difference is evident in *Otionohyus* (*Otarohyus*) *alexi*, with the larger bullae, and *Paramerycoidodon* (*Gregoryochoerus*) *wanlessi*, with the smaller bullae, both from "Zone D" of the Brule.

The inflated bullae may develop in three ways: (1) a flat inferior surface as is evident in the Merychyinae[3] and, more so, in *Merychyus* (*Metoreodon*)[4]; (2) a small but still-inflated cylindrical shape as in *Brachycrus*[5]; (3) and a depressed type which is actually divided into two portions, with an inflated area between the paroccipital and postglenoid processes and a deflated area anterior to the paroccipital process as in *Ustatochoerus.*

As previously stated, the Merycoidodontidae bullae have been of considerable interest and importance as a morphologic character throughout this revision. The internal portions of the oreodont bullae are noteworthy and have not been discussed previously. In the making of a section of a leptauchenin skull for an internal view of the facial vacuity, especially the portion

[1] Schultz and Falkenbach, 1947, fig. 13, p. 281.
[2] Schultz and Falkenbach, 1947, p. 171.
[3] Schultz and Falkenbach, 1947, p. 171.
[4] Schultz and Falkenbach, 1949, p. 232.
[5] Schultz and Falkenbach, 1940, p. 218.

that extends into the orbit cavity, a bulla was cut in half and found to be hollow. It had been known that the bullae of *Ustatochoerus* (the last-known occurrence of the oreodonts) were filled with bony structure. The fact that both hollow and filled bullae had been found prompted further investigation.

In order not to destroy the various bullae, especially since some were attached to skulls that were holotypes, natural breaks on the bullae were utilized for the sections, and other bullae were partially sawed. Since there were various sizes and shapes of bullae, and it was desirable to preserve as much of the specimens as possible, the 12 illustrated sections (fig. 55) are not drawn from exactly the same orientation. Essentially, the sections have all been made by cutting off the inferior portions of the bullae. The sectioned piece cut from the skull has been drawn, with shading, in a natural position, with the anterior borders of the bulla pointing down on the figure. Then a lateral cross section was drawn of the shaded section, and the bone-filled area was blacked in to show bulk.

The sections indicate that the early (geologic) forms have hollow auditory bullae, which gradually evolved to nearly filled bullae in the late oreodonts. There are also indications that the bullae of all phyla of oreodonts did not evolve at the same rate (apparent in fig. 55). *Desmatochoerus h. geringensis* from the Gering Formation has a bulla that is more filled in than is the example of *Desmatochoerus* (*Paradesmatochoerus*) *monroecreekensis* from the Monroe Creek Formation.

This particular portion of the study is not to be considered as conclusive. With the few sections made, the above trend is apparent. However, the degree of individual variation must be considered, and also the changes in the auditory bullae from one geologic stage to another within given phyla must be known. These will require considerable preparation, and many sections will be needed. Also, a method must be devised to insure the uniformity of the sections.

It is noteworthy that Osborn and Wortman[1] discussed the bulla in reference to its vertical distribution in the Oligocene sequence: "It is stated by Scott[2] upon the authority of Marsh,[3] that in the Oreodons from the John Day horizon the thumb is absent and that the bullae are inflated . . . He does not apparently regard the species with the inflated bullae from the White River formation as belonging to this genus [*Eporeodon*], and criticises Marsh for proposing the genus upon the ground of the inflation of the bullae. He remarks further that the forms with the large bullae occur together with those of the uninflated bullae in the same strata. This is not borne out by our observations . . . but it is a fact, abundantly demonstrated by our collection, that the greatly inflated bulla type, . . . comes *only from the upper or Protoceras Beds*. In a like manner those species in which the bullae are little or not at all inflated, . . . are confined to the lower part of the Oreodon Beds . . . These facts are significant, and seem to demonstrate very conclusively that the range in time corresponds with the evolution of the bullae."

Sinclair[4] gave a tabulation of occurrence of the various oreodonts collected in South Dakota. It is of interest that 32 examples of *Merycoidodon culbertsonii* with the minute bulla were confined to the "Lower Nodular Layer," the oreodont faunal "Zone A" of the Brule. Three examples of *Genetochoerus periculorum* with small bullae were also confined to "Zone A," and one was confined to the "Upper Nodular Layer." One wonders if the bulla was present in his "one" example, and if it may not have been an example of *G.* (*Osbornohyus*) *chamberlaini* from "Zone D" with an inflated bulla.

Oreodon gracilis was reported from both the "Lower and Upper Nodular Layer," which is understandable, as *gracilis* belongs to the Miniochoerinae, which retained the small (minute) bullae throughout their geologic history. Examples of *"Eporeodon" bullatus* were reported by Sinclair from throughout the geologic sequence. Perhaps the identification was based on material lacking the bulla.

Sinclair (p. 127) disagreed with Osborn and Wortman and reported: "From the presence of eporeodons (*E. major*) with greatly distended bullae in the *Protoceras* beds, and of forms with small rugged bullae in the *Oreodon* beds,

[1] 1894, p. 218.
[2] "Morpholog. Jahrbuch, Vol. XVI, p. 339."
[3] "Notice of New Tertiary Mammals, Amer. Jour. Sci., Vol. IX, p. 239-250."
[4] 1924, p. 101.

with a single example of the transitional form *O. bullatus* from beds of intermediate position, Osborn and Wortman were led to suggest . . . that the range in time corresponds with the evolution of the bullae. This, however, is not the case, for typical *Eporeodon bullatus,* agreeing absolutely with Fig. 5C of Osborn and Wortman's paper, occurs in both noduliferous horizons of the *Oreodon* beds and probably in the *Protoceras-Leptauchenia* beds as well."

The present writers concur with Osborn and Wortman's conclusion, except for the Miniochoerinae (which retained a small [minute] bullae throughout their life span) and the Leptaucheniinae (which had well-inflated bullae throughout theirs).

Variation in Vacuities[1]

TICHOLEPTINAE

Ustatochoerus examples from the Valentine and lower Ash Hollow have a facial vacuity bounded by the maxilla, frontal, and lacrimal bones (no contact with the nasal.) (The examples of *Ustatochoerus* from the middle Ash Hollow lack the vacuity.)

In *Ticholeptus,* the facial vacuity is bounded by the maxilla, frontal, and lacrimal bones.

MERYCHYINAE

In *Merychyus, M. (Metoreodon),* and *Paramerychyus,* the facial vacuity is bounded by the maxilla, frontal, and lacrimal bones.

In *Oreodontoides* (the facial vacuity questionably present in some examples) and *O. (Paroreodon),* the facial vacuity is bounded by the maxilla, frontal, and lacrimal bones.

PHENACOCOELINAE

In *Phenacocoelus kayi, Phenacocoelus typus, Hypsiops,* and *Submerycochoerus,* the facial vacuity is bounded by the maxilla, frontal, and lacrimal bones; in *Phenacocoelus typus* the supraorbital vacuity is completely within the frontal bone.

DESMATOCHOERINAE

Desmatochoerus, D. (Paradesmatochoerus), and *Pseudodesmatochoerus* examples may or may not have a facial vacuity bounded by the maxilla, frontal, and lacrimal bones.

Megoreodon, Desmatochoerus, D. (Paradesmatochoerus), and *Pseudodesmatochoerus* all have exoccipital vacuities.

LEPTAUCHENIINAE

All examples of the subfamily possess expanded facial vacuities that invade the nasal bone to a great degree; the maxilla, frontal, and lacrimal, to a lesser degree. The vacuity is unique in that it also invades the anterior orbital wall. See figure 54 (p. 470) for typical examples of the vacuities.

Effects on Variation of Geologic and Geographic Occurrences

Geologic Variation: Geologic variation is considered from two approaches: (1) two deposits may be recognized as belonging to one member of a formation, but one may be from the lower part while the other is from the upper part of the same member; and (2) a species may continue through two different formations or members without any noticeable change in characters. Usually oreodonts secured from the lower and upper part of a member of a formation show geologic variation. This is demonstrated in *Ustatochoerus medius,*[2] in which the size range is different in examples from the base of the Valentine Formation from what it is in those from the Burge channels at the top of the Valentine. In *Megoreodon grandis loomisi*[3] from the Gering and the Monroe Creek formations the geologic range of a species was greater than usual. In the leptauchenins, most of the forms from the lower Gering Formation are specifically different from those of the upper Gering, i.e., in the five distinct phylogenetic lines recognized by the present writers.

The above illustrates another example of the importance of field data. If one were to base a classification on morphological characters alone, often specimens from several different formations from a general locality would be considered to belong to one species, and the variations would be assumed to be individual.

Geologic variation may also be found in assemblages from two separate quarries, both within a member of a formation. This is demonstrated in a chart on *Brachycrus siou-*

[1] Genera or subgenera not mentioned lack a vacuity. Examples within a species may or may not have the vacuity.

[2] Schultz and Falkenbach, 1941, p. 23.

[3] Schultz and Falkenbach, 1954, pp. 171–174.

ense,[1] in which the maximum and minimum of several skull measurements from two different upper Miocene quarries were shown. The minimum measurement is invariably lower in the examples from Echo than in those from Humbug quarry, which apparently indicates that part of Echo quarry was of later deposition than Humbug quarry, as the sequence in *Brachycrus* became smaller.

GEOGRAPHIC VARIATION: Geographic variation may be two-fold: (1) localities that have deposits of slightly different geologic age resulting in a different size range for examples representing the same species; and (2) widely separated localities where independent development took place in the same species or genus. In the first instance the size variation of the specimens from two localities may be well within the expected variation of a species. In the second case it is difficult to determine if individual variation were involved, or if independent development took place. This difficulty is demonstrated in *Brachycrus*[2] from the Sheep Creek Formation of western Nebraska in which the earliest form, *B. wilsoni*, from the lower part of the deposits ("Sheep Creek") is larger than the later *B. siouense* from the upper part ("Lower Snake Creek"). Specimens from the Sweetwater River area of Wyoming in the Rocky Mountain region, however, present the usual phylogenetic sequence (the earliest form is the smallest). In this area the smallest (*B. rusticus*) is found at the base of the escarpment, whereas the largest (*B. sweetwaterensis*) is from the top of the same escarpment. It may be that the direct ancestors of *B. rusticus* had migrated from the plains area to the mountains to the west, where the forms became isolated from other localities. It is difficult to believe that *B. siouense* and *B. rusticus* are mere geographic varieties, even though size and other morphologic characters are similar.

COMPARISON OF VARIATIONS IN THE MERYCOIDODONTIDAE WITH THOSE IN THE RECENT PECCARIES

As there are no living forms of the Merycoidodontidae, the revisers have checked the individual and geographical variations in several different groups of living mammals. The living peccary has been considered the most similar, yet, in close observation, there seems to be little similarity. The peccaries are certainly a more homogeneous group than the oreodonts. The fossil peccary group no doubt bears evidence of many changes throughout its geologic history but not to the extent of that in the oreodonts.

The oreodonts varied from very small to comparatively large animals, ranging from the size of a recent cottontail rabbit to that of a large-sized domestic pig. The skulls varied in possessing: long or short nasals; facial and occipital vacuities (in some cases absent); low or comparatively high skulls; broad or narrow skulls; high or low zygomatic arch and brachyodont or hypsodont dentition.

The above variation is well documented, but the dental formula remained the same, $I\frac{3}{3}$, C/C, $P\frac{4}{4}$, and $M\frac{3}{3}$, with the exception of that of some of the leptauchenins, in which an incisor was lost.

The skeletal elements change in size and proportion, but no more than would be expected in any group. However, the skeletal diversity is that some of the Oligocene forms had a five-toed manus. No evidence indicates a five-toed pes at any time.

In the oreodonts sex is not readily distinguishable. In some forms (such as *Ustatochoerus*) it seems that the heavier skull represented a male example. In others it is suggested that the wider skull with the deeper malar may be the male. In the recent peccary it is found that a small male and large female skull may have the same length. The width of the peccary skulls is of no help, as there is little or no difference between the measurements of male and female examples. One female specimen has a longer C/–M^3 measurement than does either of the males. The male examples definitely have deeper malars below the orbit.

The writers considered publishing a chart on recent peccary measurements but decided that one group is not indicative of what occurs in another, especially in any comparison of a recent group of mammals with a fossil group. In the latter, one must also consider geologic variation which is not involved in any recent species.

[1] Schultz and Falkenbach, 1940, p. 240.
[2] Schultz and Falkenbach, 1940, pp. 232–254.

EXPLANATION OF CITED MEASUREMENTS

FIGURE 56 ILLUSTRATES the method of taking the measurements used in the various tables throughout the revisions of the subfamilies of the Merycoidodontidae by the present authors. These measurements are, however, not the total number taken during this study.

We realized that it is almost impossible for two persons to measure the same points and to arrive at exactly the same answer. After many years of working together, Schultz and Falkenbach came very close to the same answer. In a 100-mm. measurement, a discrepancy of 0.5 mm. or 1.5 mm. is not of importance. None of the proposed divisions in species is based on such close measurements. They are based (where measurements are concerned) on the mean.

In a phylogenetic study, measurements are extremely important, but there usually is overlapping from species to species. That is, for example, the size range of a form from the Gering Formation may be from 200 to 250 mm., whereas a form of the same line from the Monroe Creek may have a range of 240 to 290 mm.. The overlap of size range is, and should be, expected. However, if the geologic occurrence of the specimens within the overlap (in lines in which the morphologic characters are somewhat static and changes between species of subspecies are slight) is not known, they may be referred to either form.

In some groups measurements alone are not diagnostic. An example of this particular type of phylogeny is in *Merycochoerus* (chart 14, p. 416). The examples used as the basis of the chart show that, in over-all length, *M. matthewi* from the lower part of the Marsland Formation is the smallest; *M. p. magnus* from the middle Marsland is the largest; and *M. proprius* from the upper Marsland is medium-sized, instead of being the largest as would be expected. However, when other measurements of the same three examples are considered, a simple phylogeny is represented. This is obvious in the lengthening of the premaxillae; the shortening of the nasal, as well as the anterior retraction; and in the proportions in the height of the postorbital portion of the skull.

It should be noted, however, that the above facts are not the criteria for other lines of oreodonts. For instance, in *Megoreodon,* examples of *M. fricki* have a decidedly shorter skull, in over-all measurements, than do those of *M. grandis loomisi,* yet the lengths of the dental series are approximately the same. In the Desmatochoerinae, there are also examples in two lines that change in over-all skull measurements from one geologic zone to the next later zone. There are also morphologic characters that show slight changes in these same lines.

EXPLANATION OF TEXT FIGURES 54–56

FIG. 54. Lacrimal area of skulls (in outline, stipple represents vacuities): *Ustatochoerus medius* (Leidy), referred, F:A.M. 33591, from Valentine Formation, Nebraska; *Ticholeptus tooheyi* Schultz and Falkenbach, holotype, U.N.S.M. 1-15-9-36, from "Sheep Creek" Formation, Nebraska; *Desmatochoerus curvidens gregoryi* (Loomis), referred, F:A.M. 37211, from Harrison Formation, Wyoming; *Submerycochoerus bannakensis* (Douglass), referred, F:A.M. 34317, from Harrison Formation, Montana; *Phenacocoelus kayi* Schultz and Falkenbach, holotype, F:A.M. 33660A, from Harrison Formation, Wyoming; *Hypsiops brachymelis petersoni* (Loomis), referred, F:A.M. 33313, from Harrison Formation, Wyoming; *Paramerychyus harrisonensis* (Peterson), referred, F:A.M. 33314, from Harrison Formation, Wyoming; *Merychyus crabilli* Schultz and Falkenbach, holotype, F:A.M. 45384B, from Harrison Formation, Nebraska; *Merychyus crabilli ziaensis,* new subspecies, holotype, F:A.M. 72329, from equal to Harrison Formation, New Mexico; *Hadroleptauchenia densa* (Loomis), referred, F:A.M. 56959, from upper Gering Formation, Wyoming (the arrow indicates that the vacuity extends through the anterior orbital wall); *Desmatochoerus (Paradesmatochoerus) wyomingensis* Schultz and Falkenbach, holotype, F:A.M. 33312, from Gering Formation, Wyoming. ×½. FR, frontal; FV, facial vacuity; LA, lacrimal; MA, malar; MAX, maxilla; NA, nasal.

FIG. 55. Comparison of the internal surface of the auditory bullae of certain examples of the Merycoidodontidae. The shaded drawing is looking down into the interior portion of the bullae, with the anterior of the bullae at the lower portion of the drawings and the external border to the reader's right. The partially blacked-out illustration represents a lateral section (left to right) of the shaded drawing. The black portion represents the covering of bone or bone structure which varies from a thin wall to a solid structure. The geologic sequence is also cited in order to illustrate that the earliest occurrences of bullae chambers are hollow, graduating into a completely filled-in area of bone. *Subdesmatochoerus socialis* (Marsh), referred, F:A.M. 45179, from oreodont faunal "Zone D" of Brule Formation; *Hadroleptauchenia densa* (Loomis), referred, F:A.M. 56959, from upper part of Gering Formation; *Desmatochoerus h. geringensis,* referred, F:A.M. 44931 from Gering Formation; *Megoreodon g. loomisi* (Schlaikjer), referred, F:A.M. 33301, from Gering Formation; *Mesoreodan m. sweeti* Schultz and Falkenbach, referred, F:A.M. 45432, from Gering Formation; *Desmatochoerus (Paradesmatochoerus) monroecreekensis* Schultz and Falkenbach, holotype, F:A.M. 37551, from Monroe Creek Formation; *Merycoides n. blairi* Schultz and Falkenbach, referred, F:A.M. 45424, referred, from Monroe Creek Formation; *Merycochoerus proprius* Leidy, referred, F:A.M. 43016A, from the upper part of Marsland Formation; *Merychyus minimus* Peterson, referred, F:A.M. 44547, from the lower part of Marsland Formation; *Brachycrus siouense* (Sinclair), referred, F:A.M. 36112, from "Lower Snake Creek" deposits; *Merychyus (Metoreodon) relictus* Matthew and Cook, referred, F:A.M. 43078, from "Lower Snake Creek" deposits; *Ticholeptus hypsodus* Loomis, referred, U.N.S.M. 42-1-9-40, from "Lower Snake Creek" deposits. ×1.

FIG. 56. The skull and mandible are shown in outline in order to indicate the points of measurement used for all tables in this revision of the Merycoidodontidae.

Loomis (1925) used a descriptive nomenclature for the dentition; Thorpe (1937) used the tritubercular nomenclature. For clarification, both are shown on the outline drawings of M^3.

SKULL

A, length (including supraoccipital crest and incisors)
B, basal length (from anterior notch of foramen magnum to posterior base of I^1)
C, width (maximum)
D, width of brain case (maximum)
E, width, interorbital (minimum)
F, distance from anterior rim of orbit to anterior base of C/
G, distance from anterior rim of orbit to supraoccipital crest
H, length of nasals
I, width of muzzle at infraorbital foramina
J, width across canines
K, length, C/–M^3 inclusive
L, length, P^1–M^3 inclusive
M, length, P^1–P^4 inclusive
N, length, M^1–M^3 inclusive
O, width of M^3 (maximum)

MANDIBULAR RAMUS

Q, length (maximum, including incisors)
R, length, /C to condyle inclusive
S, depth of jaw under coronoid
T, depth of jaw below anterior edge of M_3

U, length, /C–M_3 inclusive
V, length, P_1–M_3 inclusive
W, length, P_1–P_4 inclusive
X, length, M_1–M_3 inclusive
APF, anterior palatine foramen
B, auditory bulla
C, canine
CD, condyle
GP, postglenoid process
IF, infraorbital foramen
LF, lacrimal fossa
MA, external auditory meatus
ML, malar
M^3, third upper molar
M_3, third lower molar
NF, nasal-frontal contact
NM, nasal-maxilla contact
P^4, fourth upper premolar
P_1, first lower premolar
P_4, fourth lower premolar
PP, paroccipital process
PPF, anterior palatine foramen
PPR, posterior palatine projection
PS, postsymphysis
SOF, supraorbital foramen
ac, anterior crest
act, anterior crescent
af, anterior fossette
aic, anterior intermediate crest
al, anterior lobe
ats, anterior style
hy, hypocone
mc, medium crest
mds, medium style
me, metacone
ml, metaconule
ms, mesostyle
mts, metastyle
pa, paracone
pc, posterior crescent
pcp, primary cusp
pct, posterior crescent
pf, posterior fossette
pic, posterior intermediate crest
pl, posterior lobe
pr, protocone
ps, parastyle
pts, posterior style

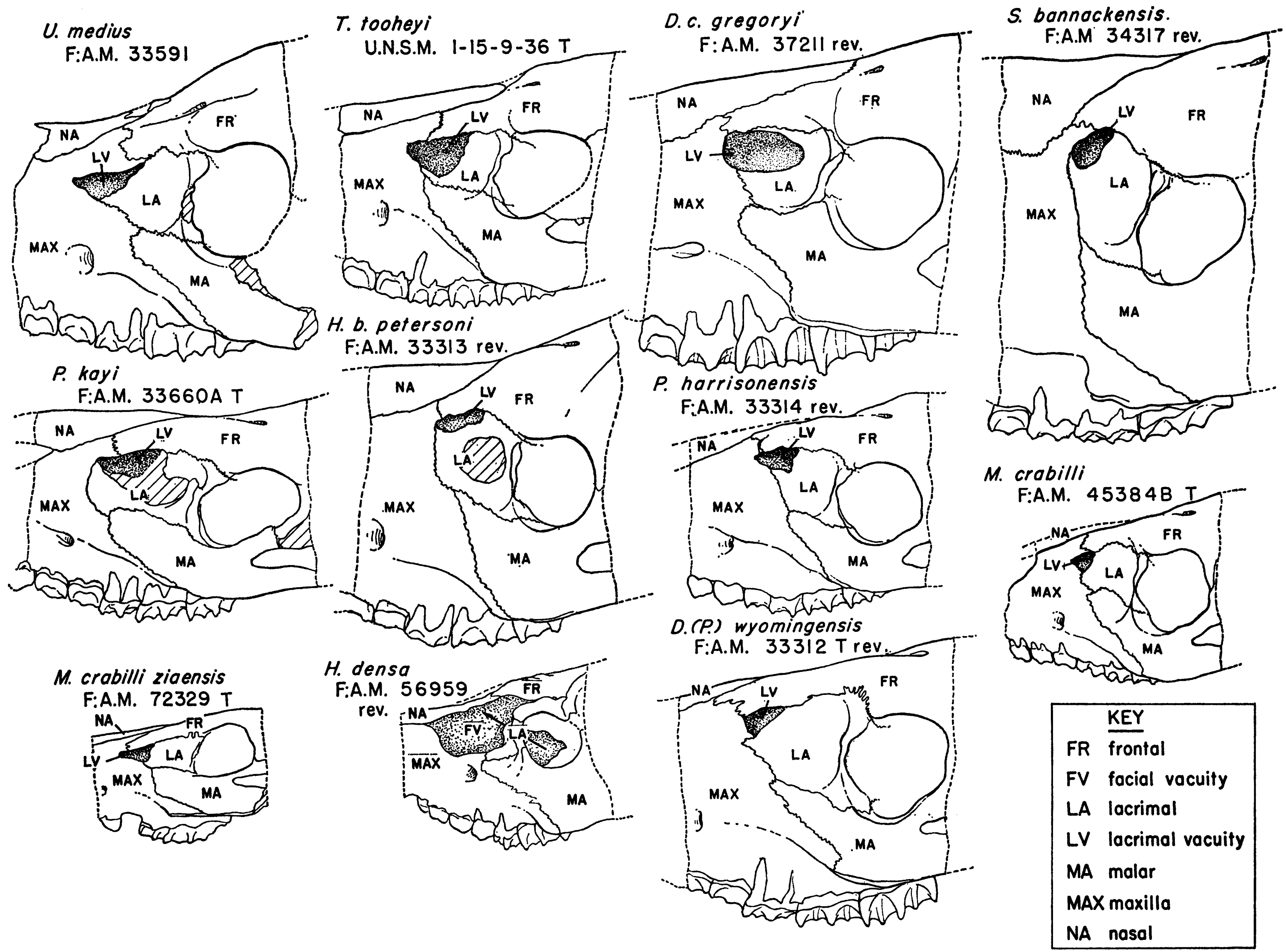


FIG. 54. Comparison of lacrimal and facial vacuities of *Ustatochoerus, Ticholeptus, Desmatochoerus, D.* (*Paradesmatochoerus*), *Submerycochoerus, Phenacocoelus, Hypsiops, Merychyus, Paramerychyus,* and *Hadroleptauchenia.* (See p. 468.) ×½.

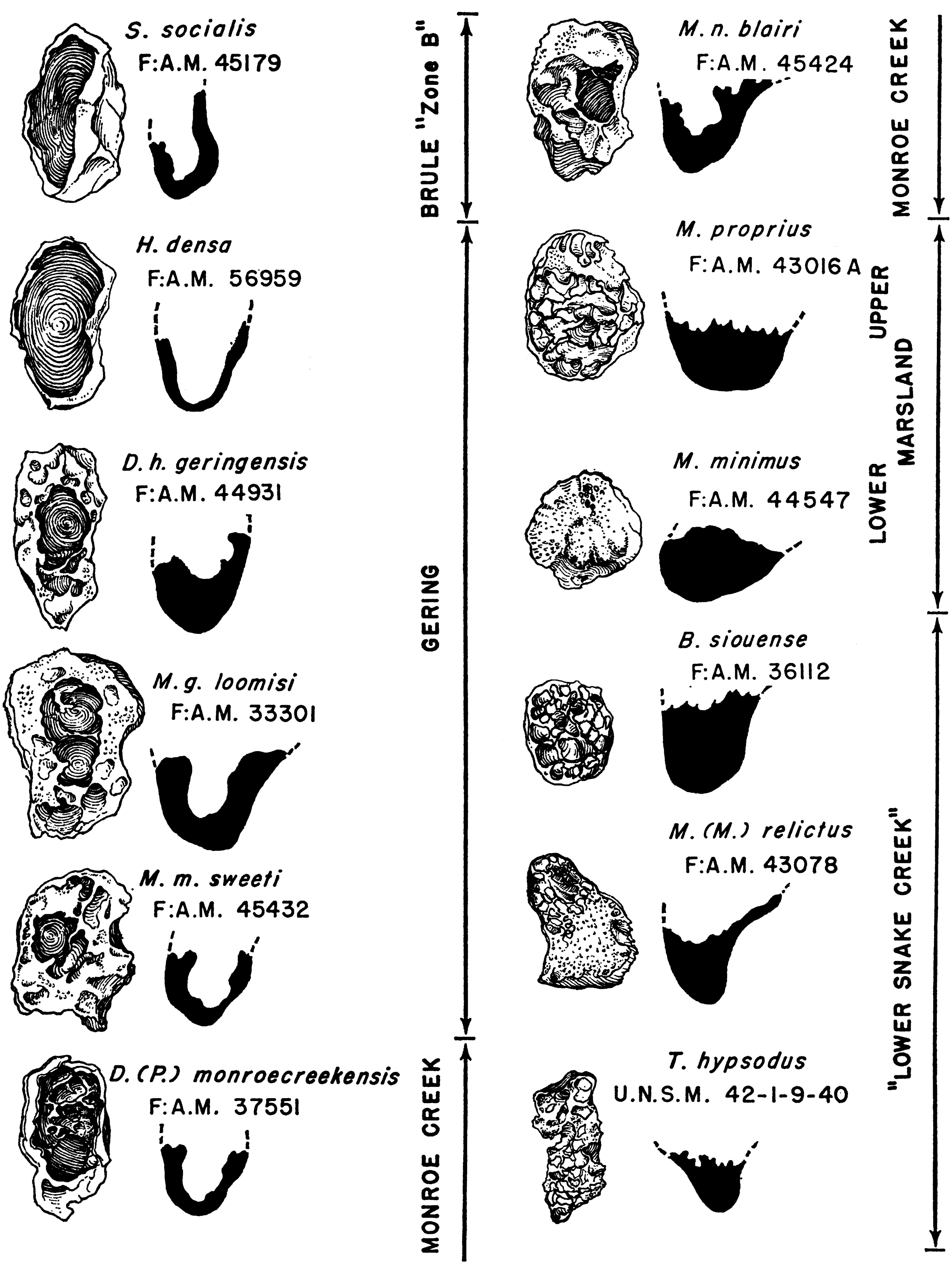


FIG. 55. Comparison of internal areas of auditory bullae in certain examples of the Merycoidodontidae. (See p. 468.) ×1.

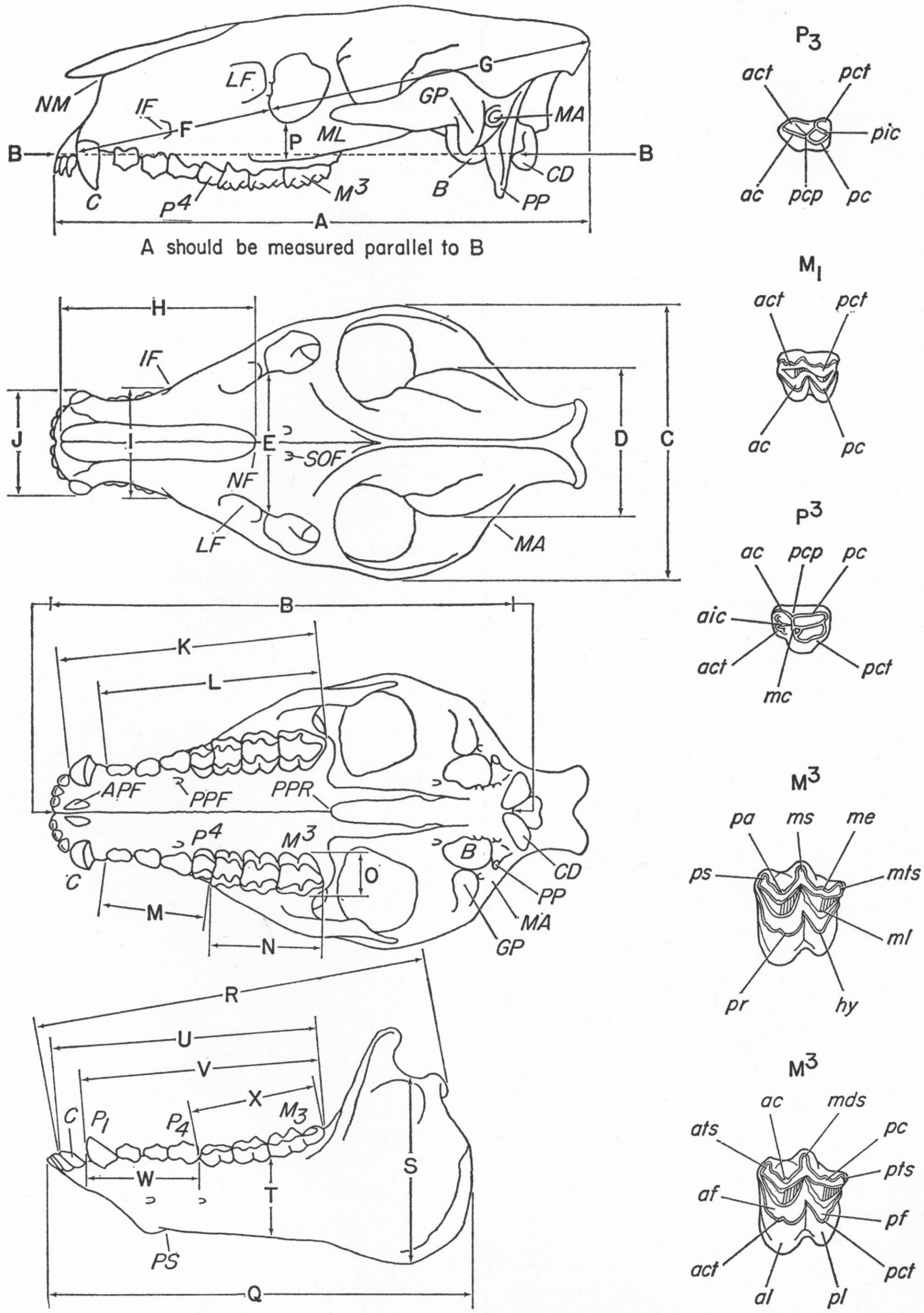


FIG. 56. Skull, mandible, P^4, M^3, P_3, and M_1 in outline, showing points of measurement and nomenclature. (See p. 468.)

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SYNOPSIS OF THE CLASSIFICATION OF THE OREODONTS (MERYCOIDODONTIDAE)

THE DATES IN THE following Synopsis refer to earlier publications on the oreodonts by Schultz and Falkenbach. Page references *without* a date refer to pages in the present report. An asterisk before a name indicates the typical species of a genus or subgenus.

Subfamily 1. Merycochoerinae Schultz and Falkenbach, 1940,[1] pp. 213–306; 1949, charts 1, 2; pp. 366–371

I. *Brachycrus* Matthew (restricted to upper Miocene[1]), 1940, p. 217

1. *B. buwaldi* (Merriam)
   1a. *B. b. barstowensis* Schultz and Falkenbach
2. *B. altiramus* (Douglass)
3. *B. elrodi* (Douglass)
4. *B. madisonius* (Douglass)
5. *B. laticeps* (Douglass)
   5a. *B. l. mooki*, new subspecies, p. 369
6. *B. siouense* (Sinclair)
7. *B. wilsoni* Schultz and Falkenbach
   7a. *B. w. longensis* Schultz and Falkenbach
8. **B. rusticus* (Leidy)
   8a. *B. r. riograndensis*, new geographic variety, p. 367
9. *B. sweetwaterensis* Schultz and Falkenbach
10. *B. vaughani* Schultz and Falkenbach
   10a. *B. v. rioosoensis*, new subspecies, p. 368

II. *Merycochoerus* Leidy (restricted to middle Miocene, 1940, p. 277)

1. **M. proprius* Leidy
   1a. *M. p. magnus* (Loomis)
2. *M. matthewi* Loomis

Subfamily 2. Ticholeptinae Schultz and Falkenbach, 1941, pp. 1–105; 1949, charts 1–2; pp. 371–376, chart 12

I. *Ustatochoerus* Schultz and Falkenbach (restricted to lower and middle Pliocene), 1941, p. 10

1. *U. californicus* (Merriam)
   1a. *U. c. raki* Schultz and Falkenbach
2. *U. compressidens* (Douglass)
3. *U. major* (Leidy)
   3a. *U. m. texanus* Schultz and Falkenbach
4. *U. medius* (Leidy)
   4a. Geographic variety
   4b. Geographic variety
   4c. *U. m. mohavensis* Schultz and Falkenbach
   4d. *U. m. novomexicanus* (Frick)
5. **U. profectus* (Matthew and Cook)
   5a. Geographic variety
   5b. *U. p. espanolensis* Schultz and Falkenbach
   5c. *U. p. studeri* Schultz and Falkenbach
   5d. *U. p. nevadaensis*, new geographic subspecies, p. 372
6. *U. skinneri* Schultz and Falkenbach
   6a. Geographic variety
7. *?U. schrammi* Schultz and Falkenbach

II. *Ticholeptus* Cope (restricted to upper Miocene)

1. *T. calimontanus* (Dougherty)
2. *T. hypsodus* Loomis
   2a. *T. h. leadorensis*, new subspecies, p. 375
3. *T. obliquidens* (Cope)
4. *T. rileyi* Schultz and Falkenbach
5. *T. tooheyi* Schultz and Falkenbach
6. **T. zygomaticus* (Cope)
   6a. *T. z. smithi* (Douglass)

III. *Mediochoerus* Schultz and Falkenbach (restricted to upper Miocene), 1941, p. 92

1. **M. blicki* Schultz and Falkenbach
2. *M. johnsoni* Schultz and Falkenbach

Subfamily 3. Merychyinae Schultz and Falkenbach, 1947, pp. 161–228; pp. 377–380

I. *Merychyus* Leidy (restricted to lower and middle Miocene), 1947, p. 171

1. *M. arenarum* Cope
   1a. *M. a. idahoensis* Schultz and Falkenbach
2. *M. calaminthus* Jahns
3. *M. crabilli* Schultz and Falkenbach
   3a. *M. crabilli ziaensis*, new subspecies, p. 377
4. **M. elegans Leidy*

[1] For the use of Oligocene, Miocene, and Pliocene, see chart 13, p. 411.

4a. Geographic variety
4b. *M. e. bluei* Schultz and Falkenbach
5. *M. minimus* Peterson
6. *M. siouxensis* Loomis
6a. Geographic variety

IA. *Merychyus (Metoreodon)* Matthew and Cook (restricted to upper Miocene), 1947, p. 232
2. **M. (M.) relictus* Matthew and Cook
1a. *M. (M.) r. taylori* Schultz and Falkenbach
1b. *M. (M.) r. fletcheri* Schultz and Falkenbach

II. *Paramerychyus* Schultz and Falkenbach (restricted to lower Miocene), 1947, p. 247
1. **P. harrisonensis* (Peterson)
2. *P. relictus* (Loomis)

III. *Oreodontoides* Thorpe (restricted to lower Miocene), 1947, p. 250
1. **O. oregonensis* Thorpe
2. *?O. curtus* (Loomis)

IIIA. *Oreodontoides (Paroreodon)* (Thorpe) (restricted to lower Miocene), 1947, p. 255
1. **O. (P.) marshi* (Thorpe)
2. *O. (P.) stocki* Schultz and Falkenbach

Subfamily 4. Promerycochoerinae Schultz and Falkenbach, 1949, pp. 73–198; pp. 450, 451, 471; 1968, figs. 49–50, 55

I. *Promerycochoerus* Douglass (restricted to lower Miocene), 1949, p. 84
1. *P. carrikeri* Peterson
2. *P. latidens* Thorpe
2a. Geographic variety
3. **P. superbus* (Leidy)
3a. *P. s. chelydra* (Cope)

IA. *Promerycochoerus (Parapromerycochoerus)* Schultz and Falkenbach (restricted to lower Miocene), 1949, p. 114
1. **P. (P.) barbouri* Schultz and Falkenbach
2. *P. (P.) macrostegus* (Cope)
2a. *P. (P.) m. furlongi* Schultz and Falkenbach

IB. *Promerycochoerus (Pseudopromerycochoerus)* Schultz and Falkenbach (restricted to lower Miocene), 1949, p. 121
1. *P. (P.) inflatus* (Thorpe)
2. *P. (P.) minor* (Douglass)
2a. *P. (P.) m. pygmyus* (Loomis)
3. **P. (P.) montanus* (Cope)
3a. Geographic variety
3b. *P. (P.) m. pinensis* Schultz and Falkenbach

II. *Mesoreodon* Scott (restricted to lower Miocene), 1949, p. 131
1. *M. cheeki* (Schlaikjer)
1a. *M. c. scotti* (Schlaikjer)
2. **M. chelonyx* Scott
2a. *M. c. wheeleri* (Koerner)
3. *M. megalodon* Peterson
3a. *M. m. sweeti* Schultz and Falkenbach
4. *?M. hesperus* (Stock)

III. *Promesoreodon* Schultz and Falkenbach (restricted to upper Oligocene), 1949, p. 152
1. **P. scanloni* Schultz and Falkenbach

IV. *Merycoides* Douglass (restricted to lower Miocene), 1949, p. 153
1. **M. cursor* Douglass
2. *M. giganteus* Schultz and Falkenbach
3. *M. nebraskensis* Schultz and Falkenbach
3a. *M. n. blairi* Schultz and Falkenbach

Subfamily 5. Phenacocoelinae Schultz and Falkenbach, 1950, pp. 91–149; pp. 451, 470

I. *Phenacocoelus* Peterson (restricted to lower and middle Miocene), 1950, p. 101
1. *P. kayi* Schultz and Falkenbach
2. *P. stouti* Schultz and Falkenbach
3. **P. typus* Peterson

II. *Hypsiops* Schultz and Falkenbach (restricted to lower Miocene), 1950, p. 113
1. **H. brachymelis* (Douglass)
1a. *H. b. petersoni* (Loomis)
2. *H. breviceps* (Douglass)
3. *H. erythroceps* (Stock)
4. *H. luskensis* Schultz and Falkenbach
5. *H. johndayensis* Schultz and Falkenbach

III. *Submerycochoerus* Schultz and Falkenbach (restricted to lower Miocene), 1950, p. 124
1. **S. bannackensis* (Douglass)

IV. *Pseudomesoreodon* Schultz and Falkenbach (restricted to lower Miocene), 1950, p. 128

1. **P. rooneyi* Schultz and Falkenbach
2. *P. rolli* Schultz and Falkenbach
3. *?P. boulderensis* Schultz and Falkenbach

Subfamily 6. Desmatochoerinae Schultz and Falkenbach, 1954, pp. 147–256; pp. 365, 451, 452, 470

I. *Megoreodon* Schultz and Falkenbach (restricted to lower Miocene), 1954, p. 163

1. *M. fricki* Schultz and Falkenbach
2. **M. grandis* (Douglass)
   2a. *M. g. loomisi* (Schlaikjer)
   2b. Geologic variety

II. *Desmatochoerus* Thorpe (restricted to Miocene), 1954, p. 177

1. **D. curvidens* (Thorpe)
   1a. *D. c. gregoryi* (Loomis)
2. *D. leidyi* (Bettany)
3. *D. hatcheri* (Douglass)
   3a. *D. h. geringensis* Schultz and Falkenbach
   3b. *D. h. grinnelli* (Koerner)
   3c. *D. h. niobrarensis* Schultz and Falkenbach
4. *D. newchicagoensis* Schultz and Falkenbach

IIA. *Desmatochoerus (Paradesmatochoerus)* Schultz and Falkenbach (restricted to lower Miocene), 1954, p. 193

1. *D. (P.) grangeri* Schultz and Falkenbach
2. *D. (P.) monroecreekensis* Schultz and Falkenbach
3. *D. (P.) sanfordi* Schultz and Falkenbach
   3a. Geographic variety
4. **D. (P.) wyomingensis* Schultz and Falkenbach
5. ?*D. (P.) thurstoni* (Stock)
6. *?D. (P.) anthonyi*, new species, p. 381

III. *Pseudodesmatochoerus* Schultz and Falkenbach (restricted to lower Miocene), 1954, p. 203

1. **P. hoffmani* Schultz and Falkenbach
2. *P. longiceps* (Douglass)
3. *P. milleri* Schultz and Falkenbach
4. *P. wascoensis* Schultz and Falkenbach
5. *?P. pariogonus* (Cope)

IV. *Superdesmatochoerus* Schultz and Falkenbach (restricted to lower Miocene), 1954, p. 213

1. **S. lulli* (Thorpe)
2. *S. microcephalus* (Thorpe)

V. *Subdesmatochoerus* Schultz and Falkenbach (restricted to middle and upper Oligocene), 1954, p. 217

1. *S. montanus* (Douglass)
2. **S. socialis* (Marsh)
   2a. *S. s. dakotensis* Schultz and Falkenbach
3. *S. shannonensis* Schultz and Falkenbach

VI. *Prodesmatochoerus* Schultz and Falkenbach (restricted to lower and middle Oligocene), 1954, p. 225

1. **P. meekae* Schultz and Falkenbach
2. *P. natronensis* Schultz and Falkenbach

Subfamily 7. Miniochoerinae Schultz and Falkenbach, 1956, pp. 377–452; 1968, p. 452

I. *Miniochoerus* Schultz and Falkenbach (restricted to middle and upper Oligocene)

1. **M. battlecreekensis* Schultz and Falkenbach
2. *M. starkensis* Schultz and Falkenbach
3. *M. nicholsae* Schultz and Falkenbach
4. *M. cheyennensis* Schultz and Falkenbach

IA. *Miniochoerus (Paraminiochoerus)* Schultz and Falkenbach (restricted to middle Oligocene), 1956, p. 402

1. **M. (P.) affinis* (Leidy)
2. *M. (P.) gracilis* (Leidy)
3. *M. (P.) helprini* Schultz and Falkenbach
4. *M. (P.) ottensi* Schultz and Falkenbach

II. *Platyochoerus* Schultz and Falkenbach (restricted to middle Oligocene), 1956, p. 425

1. **P. platycephalus* (Thorpe)
2. *P. heartensis* Schultz and Falkenbach
3. *P. hatcreekensis* Schultz and Falkenbach

III. *Stenopsochoerus* Schultz and Falkenbach (restricted to middle Oligocene), 1956, p. 435

1. **S. sternbergi* Schultz and Falkenbach
2. *S. joderensis* Schultz and Falkenbach
3. *S. berardae* Schultz and Falkenbach

IIIA. *Stenopsochoerus (Pseudostenopsochoerus)* Schultz and Falkenbach (restricted to lower and middle Oligocene), 1956, p. 443

1. **S. (P.) chadronensis* Schultz and Falkenbach
   1a. Geographic variety
2. *S. (P.) douglassensis* Schultz and Falkenbach
   2a. Geographic variety
3. *S. (P.) reideri* Schultz and Falkenbach

IV. *Parastenopsochoerus* Schultz and Falkenbach (restricted to middle Oligocene), 1956, p. 450

1. **P. coversensis* Schultz and Falkenbach

Subfamily 8. Oreonetinae Schultz and Falkenbach, 1956, pp. 453–482; 1968, pp. 366, 392, 452

I. *Oreonetes* Loomis (restricted to lower Oligocene), 1956, p. 454

1. **O. anceps* (Douglass)
   1a. *O. a. douglassi* Schultz and Falkenbach

II. *Limnenetes* Douglass (restricted to lower Oligocene), 1956, p. 461

1. **L. platyceps* Douglass

III. *Bathygenys* Douglass (restricted to lower Oligocene), 1956, p. 464

1. **B. alpha* Douglass
   1a. *B. a. hedlundae,* new subspecies, p. 386
2. *Megabathygenys goorisi,* new genus and species, p. 387
3. *Parabathygenys paralpha,* new genus and species, p. 388

Subfamily 9. Merycoidodontinae Hay (see classification, p. 5)

Subfamily 10. Eporeodontinae Schultz and Falkenbach (see classification, p. 6)

Subfamily 11. Leptaucheniini Schultz and Falkenbach (see classification, p. 6)

INDEX TO THE REVISION OF THE OREODONTS (MERYCOIDODONTIDAE)

IN THE INDEX that follows the dates refer to earlier publications on the oreodonts by Schultz and Falkenbach; the 1968 date refers to the present report. Brackets and quotation marks are used to indicate a synonym. Names in parentheses are those of subgenera. Names in boldface are new.